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*On the cover:* Stages in drawing the palate of the extinct side-necked turtle, *Stereogenys cromeri* Andrews, 1901 (tribe Stereogenyini, family Podocnemididae) from the Qasr el-Sagha Fm., late Eocene, Fayum Depression, Egypt, by Frank Ippolito.

GAFFNEY ET AL.: THE FAMILY PODOCNEMIDIDAE

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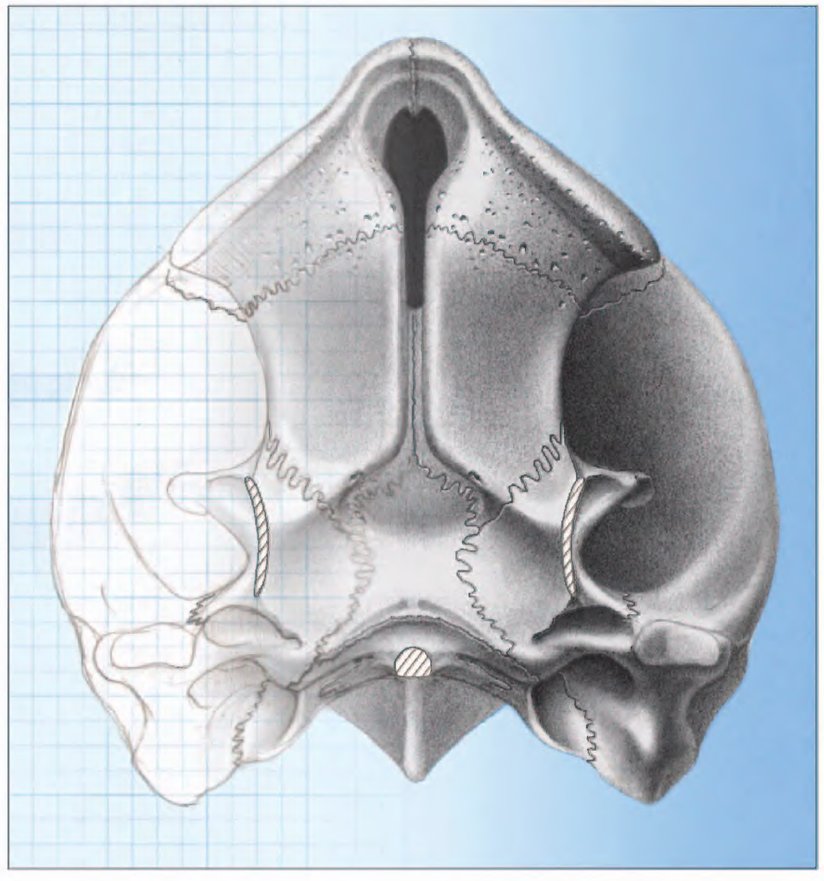
# Evolution of the Side-necked Turtles: The Family Podocnemididae

Eugene S. Gaffney, Peter A. Meylan, Roger C. Wood, Elwyn Simons, and Diogenes de Almeida Campos



Bulletin of the American Museum of Natural History

# EVOLUTION OF THE SIDE-NECKED TURTLES: THE FAMILY PODOCNEMIDIDAE

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## ABSTRACT

The family Podocnemididae consists of 20 genera and 30 species considered here as valid and diagnosable by cranial characters. Three of these genera and eight species persist into the Recent fauna, barely reflecting the evolutionary diversity and distribution of the group. The family extends from the Late Cretaceous to the Recent and occurs in North and South America, Europe, Asia, and Africa. A phylogenetic analysis utilizes 31 podocnemidid taxa (30 named and one unnamed; a total of 37 taxa analyzed includes outgroups) in the Podocnemididae that are analyzed using PAUP. The resulting consensus of nine equally parsimonious cladograms is the basis for a new classification of the family. The family Podocnemididae is reconfirmed as monophyletic, using the unique possession of a cavum pterygoidei formed by the basisphenoid, pterygoid, prootic, and quadrate, underlain by the pterygoid and basisphenoid, among other characters. Much of our resolution agrees with that of França and Langer (2006), which can be modified and restated as follows: (*Bauruemys* (*vilavilensis* (*Podocnemis* (*Peltocephalus, Erymnochelys*)))). The two clades proposed by Broin (1991) and Lapparent de Broin (2000b, 2001, 2003a, 2003b), designated by her as the "subfamily Podocnemidinae" and the "subfamily Erymnochelinae," are inconsistent with our analysis. In our analysis the "Podocnemidinae" (sensu Broin, 1991) is paraphyletic, and the "Erymnochelinae" (sensu Broin, 1991) could be made monophyletic, with the important addition of *Peltocephalus* (placed in the "Podocnemidinae" by Broin).

We add a number of new taxa to the basal Podocnemididae and to the broad-jawed subtribe Stereogenyina. Within the family Podocnemididae Cope, 1868, the sister taxon to all other podocnemidids and recognized as the subfamily Bauruemydinae, new, is *Bauruemys elegans* (Suárez, 1969a), known from associated skulls and shells. All other podocnemidids, the redefined subfamily Podocnemidinae Cope, 1868, are united by a slight to absent temporal emargination, a completely closed foramen jugulare posterius, and saddle-shaped cervical centra (modified as a separate state in *Erymnochelys*). A basal group of Cretaceous-Paleocene podocnemidids that are the sister group to all remaining podocnemidids, here termed the infrafamily Peiropemydodda, consisting of two taxa from the late Cretaceous of Brazil, *Peiropemys mezzalirai,* n. gen. et sp., and *Pricemys caiera,* n. gen. et sp., and *Lapparentemys vilavilensis* (Broin, 1971), n. gen., from the Paleocene of Bolivia. The resolution of the basal members of the family is: (*Bauruemys* (*Pricemys* (*Lapparentemys, Peiropemys*)) (Infrafamily Podocnemidodda)).

The remaining podocnemidids form the infrafamily Podocnemidodda Cope, 1868, new rank, and is characterized by the possession of a cheek emargination that does not reach above the level of the orbit, the medial expansion of the triturating surfaces with a median maxillary ridge present, and the presence of accessory ridges on the triturating surfaces. This group contains the living podocnemidids and a series of extinct forms, including the marine broad-jawed taxa.

Within the Podocnemidodda, the genus *Podocnemis* is the sister group to all the remaining taxa, which is the magnatribe Erymnochelydand. When only the living fauna is considered our results show *Podocnemis* as the sister taxon to *Erymnochelys* plus *Peltocephalus*, in common with Williams (1954c), França and Langer (2006), Meylan et al. (2009), and Cadena et al. (2010). With the fossil taxa present, the Erymnochelydand is united only by the small to absent cheek emargination. However, some of the fossil taxa (i.e., *Caninemys*, *Dacquemys*), are not known for a number of characters, and, if the analysis is reduced to include only the living species, *Erymnochelys* and *Peltocephalus* are united by a greater number of characters: cavum pterygoidei with enlarged anterior opening, so that the foramen cavernosum enters the roof of the cavum pterygoidei, orbits facing anterolaterally, jugal-quadrate contact present, cheek emargination slight to absent, horizontal occipital shelf absent, premaxillae reach apertura narium interna (also in some *Podocnemis*), supraoccipital roof exposure slight or absent, chorda tympani enclosed in processus retroarticularis, neural series extends to costal six, and axillary musk duct not in bridge.

When one considers just the Recent genera, none of the published molecular results reproduce the Gaffney and Meylan (1988) and Lapparent de Broin (2000b) resolution of (*Erymnochelys* (*Podocnemis, Peltocephalus*)); rather these publications show a preference for the (*Peltocephalus* (*Podocnemis, Erymnochelys*)) arrangement, while we, in agreement with França and Langer (2006) and the earlier version of the present data set, Meylan et al. (2009), place our marbles with the third alternative, (*Podocnemis* (*Peltocephalus, Erymnochelys*)). This latter hypothesis has a

number of characters favoring its resolution, even when fossils are excluded. One of the more compelling ones is the large cavum pterygoidei with an enlarged anterior opening and the foramen cavernosum containing the lateral head vein, entering the roof of the cavum pterygoidei.

Within the magnatribe Erymnochelydand are the following taxa: *Caninemys*, *Dacquemys*, unnamed genus UCMP 42008, *Albertwoodemys, Turkanemys, Peltocephalus, Erymnochelys*, *Neochelys*, *Papoulemys*, and the members of the tribe Stereogenyini (see below). The resolution of *Caninemys* within the Erymnochelydand is not strongly supported; in only one step it becomes a multichotomy with *Podocnemis* and the infrafamily Peiropemydodda. *Neochelys, Papoulemys* (possibly a synonym of *Neochelys*), and *Dacquemys*, however, are strongly supported as part of the magnatribe Erymnochelydand, as proposed earlier (Broin, 1991; Lapparent de Broin, 2000b, 2001, 2003a, 2003b).

A new shell-based taxon, *Albertwoodemys testudinum,* n. gen. et sp., and an unnamed skull and shell, UCMP 42008, are united by a high-domed shell with thick lateral ridges along the plastron and the absence/fusion of the pectoral scales. The skull of UCMP 42008 agrees with that in *Dacquemys* in having large parietals and a supraoccipital covering the posterior margin. Lacking a skull, *Albertwoodemys* is not entered into the data set, but the skull-shell specimen of the closely related UCMP 42008 is in the analysis.

New skull material identifiable as *Neochelys* has been discovered associated with shells of *"Podocnemis" fajumensis* Andrews, 1903, resulting in the new combination *Neochelys fajumensis* (Andrews, 1903). *Neochelys* has the Erymnochelydand synapomorphy of a large cavum pterygoidei with an enlarged anterior opening and the foramen cavernosum entering the roof of the cavum pterygoidei, as in *Peltocephalus* and *Erymnochelys.* The European *Neochelys* species are Eocene and the African Fayum species is Early Oligocene, extending both spatial and temporal ranges of the genus.

The tribe Stereogenyini has a dorsal process of the palatine that reaches the frontal in the septum orbitotemporale, the fossa precolumellaris is absent, and both foramina nervi hypoglossi are combined and recessed in a short canal that opens on the occipital surface. Within the tribe Stereogenyini, *Mogharemys blanckenhorni* Dacqué (1912), n. gen., is the sister taxon to the well-defined subtribe Stereogenyina.

Two groups are recognized within the subtribe Stereogenyina. The infratribe Bairdemydita contains *Bairdemys* Gaffney and Wood, *Latentemys plowdeni,* n. gen. et sp., *Cordichelys antiqua* (Andrews, 1903), n. gen. The infratribe Stereogenyita contains *Brontochelys gaffneyi* (Wood, 1970), n. gen., *Lemurchelys diasphax,* n. gen. et sp., *Shweboemys* Swinton, 1939, and *Stereogenys* Andrews, 1901. The subtribe Stereogenyina is strongly supported by a secondary palate with a median cleft, unique among turtles, as well as other characters. While the other Podocnemididae were apparently freshwater species, there is evidence that many or all of the subtribe Stereogenyina were marine or near-shore marine.

Compared with a group such as the Bothremydidae, we see in the evolution of the Podocnemididae, a relatively conservative series of South American paraphyletic taxa with an unusually persistent cranial as well as shell morphology, beginning in the Late Cretaceous with *Bauruemys, Peiropemys,* and *Pricemys,* and continuing with the Paleocene *Lapparentemys,* culminating in the Recent *Podocnemis.* A monophyletic Tertiary group with more geographic, taxonomic, and morphologic diversity, the magnatribe Erymnochelydand, contains African, European, Asian, and South American taxa, as well as a radiation of marine, broad-jawed species in the mid-Tertiary. The living remnants of the Erymnochelydand are the South American *Peltocephalus* and the African *Erymnochelys,* close relatives despite their current geographic separation.

## INTRODUCTION

The Cretaceous to Recent pleurodire family Podocnemididae occurs in North and South America, Europe, Asia, and Africa, although the surviving species are restricted to South America and Madagascar. The fossil record shows that the wider group, the epifamily Podocnemidinura, containing podocnemidids plus their near relatives, extends back to the early Cretaceous in South America. The living species are freshwater, but the fossil record shows that a predominantly marine/near-shore marine clade, the

subtribe Stereogenyina, was present in the Tertiary of northern South America, the North American coastal plain, the Caribbean, northern Africa, and western Asia (Burma).

The present paper is a documentation and phylogenetic analysis of the family Podocnemididae, and is a direct continuation of Gaffney et al. (2006). It is very similar in purpose, scope, and treatment. We rely on the Introduction, Previous Work, Organization, and Systematics sections of Gaffney et al. (2006), which all contain explanatory information pertaining to the present paper that is not repeated here. Treatment of the higher categories above the family Podocnemididae are also in Gaffney et al. (2006); diagnoses, phylogenetic analyses, and literature for these taxa are not repeated here. This paper focuses on the family Podocnemididae.

We name nine new genera and describe the skulls of 11 genera. Additionally, the shell morphology of some South American Cretaceous and Paleocene taxa is described, including some with skull-shell associations. All of the named podocnemidids that are represented by diagnosable material are treated and diagnosed. We discuss a series of diagnosable taxa that are not phylogenetically resolvable in our analysis and are referred to as Podocnemididae, incertae sedis. A further eight taxa, often referred to the Podocnemididae, are undiagnosable and considered nomina dubia. The analysis relies mostly on cranial characters and taxa known only from the shell are poorly resolved in our analysis.

Although we present our conclusions as a phylogenetic analysis, the description and documentation of the morphology of these taxa is our primary purpose, as it was in Gaffney et al. (2006). The newly described material is mostly from two groups, the so-called "basal" South American Cretaceous-Paleocene Podocnemididae, here termed the infrafamily Peiropemydodda, lying outside the common ancestor of the living species, and the mid-Tertiary, broad-jawed, presumably brackish to marine, tribe Stereogenyini. We also include new figures and comparative information about other Podocnemidinura (i.e., *Neochelys, Hamadachelys,* and some of the recent species of *Podocnemis*). We do not review alpha-level problems within the Recent species of Podocnemididae; rather, we emphasize documentation of the previously undescribed or poorly known fossil taxa that are represented by newly discovered skulls or skull-shell associations.

One of the serious problems in analyzing these podocnemidid taxa (and others among the Pleurodira) is the persistent referral in the literature to taxa that are diagnosable as species or some level of alpha taxon, but possess too few characters to reasonably resolve in a phylogenetic analysis that would allow them to be confidently placed within a genus or some other higher level taxon. This problem is particularly apparent for a number of shell taxa that can be diagnosed at the species level, and in some cases are named as monospecific genera, but that cannot be objectively related to groups within the family, except by arbitarily choosing one or two characters. A significant factor in this problem, repeatedly emphasized in the study of Pelomedusoides (Gaffney et al., 2006), is the conservative nature of the shell morphology of Pelomedusoides turtles. It is the broad phylogenetic distribution of this highly conserved shell morphotype that has led to the liberal use of the generic epithet "*Podocnemis*" for fossil shells, which may belong to either the Podocnemididae or the Bothremydidae. A modification of this tendency is to use some autapomorphies to raise a species to generic level. However, if the taxon still lacks enough comparative characters to use in a phylogeny, it seriously hampers analysis of the diversity that is known. Gaffney et al. (2006) dealt with this problem by placing these taxa at various levels of incertae sedis, and that is what we do here.

As part of our Podocnemididae project, the reader is directed to earlier papers on podocnemidids in this series: Gaffney et al. (1998), Gaffney et al. (2002), Gaffney and Wood (2002), Gaffney and Forster (2003), Gaffney et al. (2006), Gaffney et al. (2008), and Meylan et al. (2009). The cranial morphology of turtles and an illustrated compilation of morphologic terminology can be found in Gaffney (1972, 1979). An introduction to the cranial morphology of pleurodires can be found in Gaffney et al. (2006). Previous work on the Podocnemididae is treated below under the relevant taxa

and previous systematic work is in Phylogenetic Analysis. We restrict ourselves to studies pertaining to systematics and morphology and do not include conservation, ecology, or other biologic features of the family except where they relate to systematic problems.

### Institutional Abbreviations

| | |
|---|---|
| AMNH | American Museum of Natural History, New York, New York |
| AMU-CURS | Alcaldía del Municipio Urumaco, Colección Rodolfo Sánchez, Venezuela |
| BMNH | Natural History Museum, London, Great Britain |
| CGM | Cairo Geological Museum, Egypt |
| CPP | Centro de Pesquisas Paleontológicas "Llewellyn Ivor Price," Uberaba, Brazil |
| MAC | Musee Royale d'Afrique Centrale, Tervuren, Belgium |
| DGM | Divisão de Geologia e Mineralogia, Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil |
| DNPM | Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil |
| DPC | Duke Primate Center, Duke University, Durham, North Carolina |
| FCUS | Faculty of Sciences of the University of Salamanca, Spain |
| FMNH | Field Museum of Natural History, Chicago, Illinois |
| IGM | Instituto de Investigaciones en Geosciencias, Minería y Química, Museo Geológico Bogotá, Bogotá, Colombia |
| LACM | Natural History Museum of Los Angeles County, California |
| MACN | Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina |
| MB | Museum fur Naturkunde, Berlin, Germany |
| MCT | Divisão de Geologia e Mineralogia, Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil |
| MCZ | Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts |
| MCNC | Museo de Ciencias Naturales, Caracas, Venezuela |
| MDE | Musée de Dinosaures, Espéraza, France |
| MHNC | Museo de Historia Natural de Cochabamba, Cochabamba, Bolivia |
| MNHN | Muséum national d'Histoire naturelle, Paris, France |
| MNHNP | Paleontology, Muséum national d'Histoire naturelle, Paris, France |
| MN-V | Setor de Paleovertebrados, Departmento de Geologia e Paleontologia, Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil |
| MNRJ | Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil |
| NFWFL | National Fish and Wildlife Forensics Laboratory, Oregon |
| NMV | Naturhistorisches Museum, Vienna, Austria |
| UCMP | University of California, Museum of Paleontology, Berkeley, California |
| UFAC-PV | Laboratorio de Paleontologia, Universidade Federal do Acre, Rio Branco, Brazil |
| UFRGS | Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil |
| USNM | United States National Museum, Washington, DC |
| UF | Florida Museum of Natural History, University of Florida, Gainesville, Florida |
| WUS | School of International Liberal Studies, Waseda University, Tokyo, Japan |

### Anatomical Abbreviations

| | |
|---|---|
| ab | abdominal scale |
| acst | aditus canalis stapedio-temporalis |

| | |
|---|---|
| ana | anal scale |
| ani | apertura narium interna |
| ap | antrum postoticum |
| ax | axillary buttress |
| bo | basioccipital |
| bs | basisphenoid |
| ca | columella auris |
| cc | canalis cavernosus |
| ccr | cavum cranii |
| cl | cavum labyrinthicum |
| cos | costal bone |
| cpt | cavum pterygoidei |
| ct | cavum tympani |
| ds | dorsum sellae |
| ent | entoplastron |
| epi | epiplastron |
| ex | exoccipital |
| facci | foramen anterius canalis carotici interni |
| faf | fossa acustico-facialis |
| fc | foramen cavernosum |
| fcti | foramen chorda tympani inferius |
| fem | femoral scale |
| fio | foramen interorbitale |
| fja | foramen jugulare anterius |
| fjp | foramen jugulare posterius |
| fn | fossa nasalis |
| fnf | foramen nervi facialis |
| fnt | foramen nervi trigemini |
| fo | fenestra ovalis |
| fon | foramen orbito-nasale |
| fp | foramen praepalatinum |
| fpc | fossa precolumellaris |
| fpcci | foramen posterius canalis carotici interni |
| fpo | fenestra postotica |
| fpp | foramen palatinum posterius |
| fr | frontal |
| fst | foramen stapedio-temporale |
| gu | gular scale |
| ha | hiatus acusticus |
| hu | humeral scale |
| hyo | hyoplastron |
| hypo | hypoplastron |
| ib | inguinal buttress |
| ica | incisura columellae auris |
| ils | iliac scar |
| in | intergular scale |
| ju | jugal |
| ma | marginal scale |
| me | mesoplastron |
| mx | maxilla |
| ne | neural bone |
| nu | nuchal bone |
| op | opisthotic |
| pa | parietal |
| pal | palatine |
| pec | pectoral scale |
| per | peripheral bone |
| pf | prefrontal |
| pg | pygal bone |
| pip | processus inferior parietalis |
| pl | processus clinoideus |
| pm | premaxilla |
| po | postorbital |
| pr | prootic |
| pt | pterygoid |
| ptf | pterygoid flange |
| ptp | processus trochlearis pterygoidei |
| qj | quadratojugal |
| qu | quadrate |
| rb | rostrum basisphenoidale |
| se | sulcus eustachii |
| sf | sulcus olfactorius |
| so | supraoccipital |
| sot | septum orbitotemporale |
| spg | suprapygal |
| spt | sulcus palatinopterygoideus |
| sq | squamosal |
| st | sella turcica |
| VII | foramen nervi facialis |
| VIII | foramen nervi acustici |
| vo | vomer |
| XII | foramen nervi hypoglossi |
| xip | xiphiplastron |

## SUMMARY CLASSIFICATION

Hyperfamily Pelomedusoides Cope, 1868
Epifamily Podocnemidinura Cope, 1868
Family Podocnemididae Cope, 1868
Subfamily Bauruemydinae, new
*Bauruemys* Kischlat, 1994
*Bauruemys elegans* (Suárez, 1969a)
Subfamily Podocnemidinae Cope, 1868
Infrafamily Peiropemydodda, new
*Peiropemys,* n. gen.
*Peiropemys mezzalirai,* n. gen. et sp.
*Lapparentemys,* n. gen.
*Lapparentemys vilavilensis* (Broin, 1971), n. comb.
*Pricemys,* n. gen.
*Pricemys caiera,* n. gen. et sp.
Infrafamily Podocnemidodda Cope, 1868, new rank
Magnatribe Podocnemidand Cope, 1868, new rank
*Podocnemis* Wagler, 1830
*Podocnemis expansa* (Schweigger, 1812)
*Podocnemis vogli* Müller, 1935
*Podocnemis lewyana* Duméril, 1852
*Podocnemis sextuberculata* Cornalia, 1849
*Podocnemis unifilis* Troschel, 1848
*Podocnemis erythrocephala* (Spix, 1824)
*Podocnemis bassleri* Williams, 1956
Magnatribe Erymnochelydand Broin, 1988, new rank
*Caninemys* Meylan, Gaffney, and Campos 2009
*Caninemys tridentata* Meylan, Gaffney, and Campos 2009
*Dacquemys* Williams, 1954
*Dacquemys paleomorpha* Williams, 1954
*Albertwoodemys,* n. gen.
*Albertwoodemys testudinum,* n. gen. et sp.
UCMP 42008, unnamed new genus and species
*Turkanemys* Wood, 2003
*Turkanemys pattersoni* Wood, 2003
*Erymnochelys* Baur, 1888
*Erymnochelys madagascariensis* (Grandidier, 1867)
*Peltocephalus* Dumeril and Bibron, 1835
*Peltocephalus dumerilianus* (Schweigger, 1812)
*Neochelys* Broin, 1977
*Neochelys arenarum* Broin, 1977
*Neochelys fajumensis* (Andrews, 1903), n. comb.
*Papoulemys* Tong, 1998
*Papoulemys laurenti* Tong, 1998
Tribe Stereogenyini, new
Subtribe Mogharemydina, new
*Mogharemys,* n. gen.

*Mogharemys blanckenhorni* Dacqué (1912), n. comb.
Subtribe Stereogenyina, new
Infratribe Bairdemydita, new
*Latenemys,* n. gen.
*Latenemys plowdeni,* n. gen. et sp.
*Cordichelys,* n. gen.
*Cordichelys antiqua* (Andrews, 1903), n. comb.
*Bairdemys* Gaffney and Wood, 2002
*Bairdemys hartsteini* Gaffney and Wood, 2002
*Bairdemys venezuelensis* (Wood and Díaz de Gamero, 1971)
*Bairdemys winklerae* Gaffney et al., 2008
*Bairdemys sanchezi* Gaffney et al., 2008
Infratribe Stereogenyita, new
*Brontochelys,* n. gen.
*Brontochelys gaffneyi* (Wood, 1970), n. comb.
*Lemurchelys,* n. gen.
*Lemurchelys diasphax,* n. gen. et sp.
*Shweboemys* Swinton, 1939
*Shweboemys pilgrimi* Swinton, 1939
*Stereogenys* Andrews, 1901
*Stereogenys cromeri* Andrews, 1901

**Dubious Taxa**

Podocnemididae Incertae Sedis

*Cambaremys langertoni* França and Langer, 2005
*Cerrejonemys wayuunaiki* Cadena, Bloch, and Jaramillo, 2010
*Kenyemys williamsi* Wood, 1983
Peirópolis A, unnamed shell taxon
Peirópolis B, unnamed shell taxon
*"Podocnemis" argentinensis* Cattoi and Freiburg,1958
*"Podocnemis" geologorum* Simpson,1943
*"Podocnemis" medemi* Wood,1997
*"Podocnemis" negrii* Carvalho, Bocquentin, and Lapparent de Broin, 2002
*"Podocnemis" pritchardi* Wood, 1997
*Roxochelys wanderleyi* Price, 1953
*"Stereogenys" libyca* Andrews,1903
*Stupendemys geographicus* Wood,1976

**Taxa Nomina Dubia**

*Duerochelys arribasi* Jiménez,1975
*Latisternon microsulcae* Auffenberg, 1981
*"Podocnemis" aegyptiaca* Andrews, 1900
*"Podocnemis" bramlyi* Fourteau,1920
*"Podocnemis" brasiliensis* Staesche,1937
*"Podocnemis" freibergi* Agnolin, 2004
*"Podocnemis" harrisi* Pacheco, 1913
*"Stereogenys" podocnemoides* Reinach, 1903

## SYSTEMATICS

### Hyperfamily Pelomedusoides Cope, 1868
### Magnafamily Podocnemidera Cope, 1868
### Superfamily Podocnemidoidea Cope, 1868
### Epifamily Podocnemidinura Cope, 1868

Type Genus: *Podocnemis* Wagler, 1830.

Included Taxa: *Hamadachelys* Tong and Buffetaut, 1996; *Brasilemys* Lapparent de Broin, 2000b; *Portezueloemys* de la Fuente, 2003; and the family Podocnemididae.

Diagnosis: A member of the superfamily Podocnemidoidea uniquely possessing a cavum pterygoidei formed by basisphenoid, pterygoid, prootic, and quadrate, underlain by pterygoid and basisphenoid (in contrast to the fossa pterygoidea of some Bothremydidae); processus retroarticularis of articular oriented posteroventrally; basioccipital-opisthotic contact present (also in Pelomedusidae and some Chelidae, not known in *Brasilemys*).

Discussion: See Gaffney et al. (2006) for revised diagnoses and phylogeny of included taxa. We include here a new restoration and new figures of two specimens of *Hamadachelys escuilliei* (figs. 1–6) for comparison with Podocnemididae. A description of *Hamadachelys* can be found in Tong and Buffetaut (1996).

### Family Podocnemididae Cope, 1868

Type Genus: *Podocnemis* Wagler, 1830.

Included Genera: *Podocnemis* Wagler, 1830; *Peltocephalus* Duméril and Bibron, 1835; *Erymnochelys* Baur, 1888; *Bairdemys* Gaffney and Wood, 2002; *Dacquemys* Williams, 1954c; *Neochelys* Bergounioux, 1954; *Shweboemys* Swinton, 1939; *Bauruemys* Kischlat, 1994; *Stereogenys* Andrews, 1901; *Caninemys* Meylan, Gaffney, and Campos, 2009; *Turkanemys* Wood, 2003; *Neochelys* Bergounioux, 1954; *Papoulemys* Tong, 1998; *Peiropemys,* n. gen.; *Lapparentemys,* n. gen.; *Pricemys,* n. gen.; *Mogharemys,* n. gen.; *Cordichelys,* n. gen.; *Latentemys,* n. gen.; *Brontochelys,* n. gen.; *Albertwoodemys,* n. gen.; *Lemurchelys,* n. gen.

Incertae sedis within family: *Stupendemys,* Wood, 1976; *Cerrejonemys* Cadena et al., 2010; *Roxochelys* Price, 1953; *Cambaremys,* França and Langer, 2005; *Kenyemys* Wood, 1983.

Diagnosis: Member of the epifamily Podocnemidinura uniquely possessing a fully developed, medially extensive cavum pterygoidei with a completely developed pterygoid flange, and a dentary covered laterally by the surangular in contrast to *Brasilemys* and *Hamadachelys*; agreeing with *Hamadachelys* in basioccipital-opisthotic contact (not known in *Brasilemys*, may be at Podocnemidinura level), incisura columellae auris enclosing stapes and eustachian tube, and exoccipital-quadrate contact absent, all in contrast to *Brasilemys*; palatine forming moderate amount of triturating surface in contrast to little or none as in *Euraxemys*; pectoral scales contact epiplastra.

Discussion: We are not aware of any contrary hypothesis to podocnemidid monophyly.

#### Subfamily **Bauruemydinae**, new

Diagnosis: Member of the Podocnemididae; quadratojugal-parietal contact short; temporal emargination extensive; cheek emargination does not reach above level of orbit; foramen jugulare posterius open laterally; tuberculum basioccipitale narrowly spaced; cervical centra not saddle shaped.

Discussion: This new subfamily is created to reflect the position of *Bauruemys* as sister taxon to all other Podocnemididae. See table 1 for comparison of the basal Podocnemididae described here.

Included Taxa: *Bauruemys.*

#### *Bauruemys* Kischlat, 1994

Type Species: *Podocnemis elegans* Suárez, 1969a.

Included Species: *Bauruemys elegans.*

Distribution: Late Cretaceous of northern South America.

Revised Diagnosis: A podocnemidid known from the skull and postcrania; temporal emargination extensive, second neural consistently four sided, uniquely among the Podocnemididae; skull relatively wide and flat in contrast to *Podocnemis*, orbits facing dorsally rather than dorsolaterally as in *Podocnemis*; interorbital groove such as

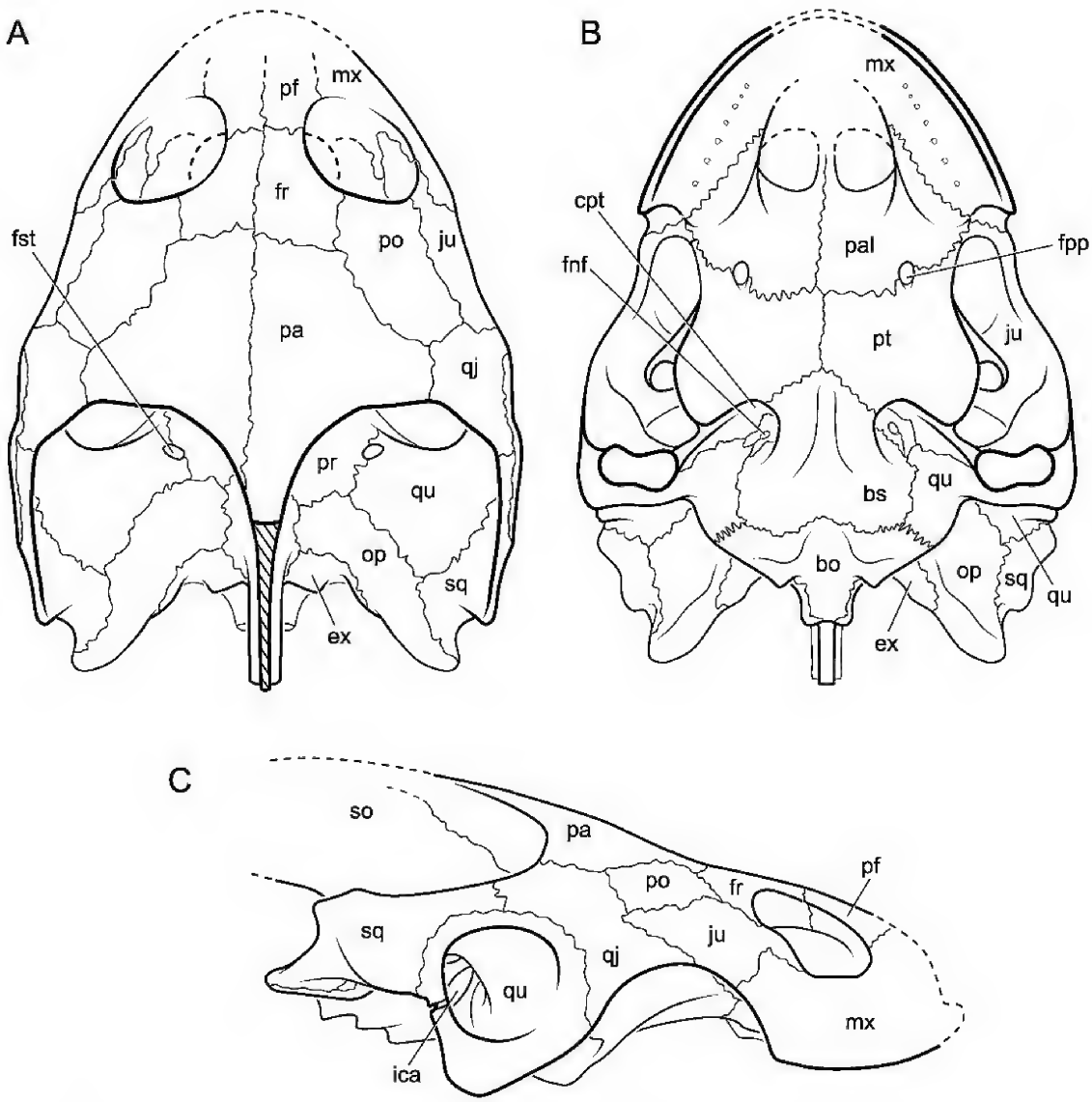



Fig. 1. *Hamadachelys escuilliei* Tong and Buffetaut, 1996. Partially restored skull based on MDE T03 and AMNH 30644. **A,** dorsal; **B,** ventral; **C,** lateral. [C. Facella, del.]

found in *Podocnemis* absent; postorbital large in contrast to *Podocnemis*; parietal-quadratojugal contact small; cheek emargination does not reach above level of orbit; medial expansion of triturating surface, median maxillary ridge, absent, wide concavity on the midline, formed by the premaxillae and anterior maxilla present; accessory ridge in triturating surface absent; vomer present; vomer-maxilla contact narrow; fossa precolumellaris deep as in *Peiropemys*; foramen jugulare posterius open laterally; basioccipital-opisthotic contact narrow in contrast to all other Podocnemididae in which it is wider; tuberculum basioccipitale not widely separated as in all other Podocnemididae; interparietal scale equilateral triangle; cavum pterygoidei with small anterior opening for foramen cavernosum; horizontal occipital shelf present as in *Podocnemis*; chorda tympani not enclosed in processus retroarticularis; cervical centra not saddle shaped. See table 1.

Small shell (less than 150 mm carapace length) differing from other South American

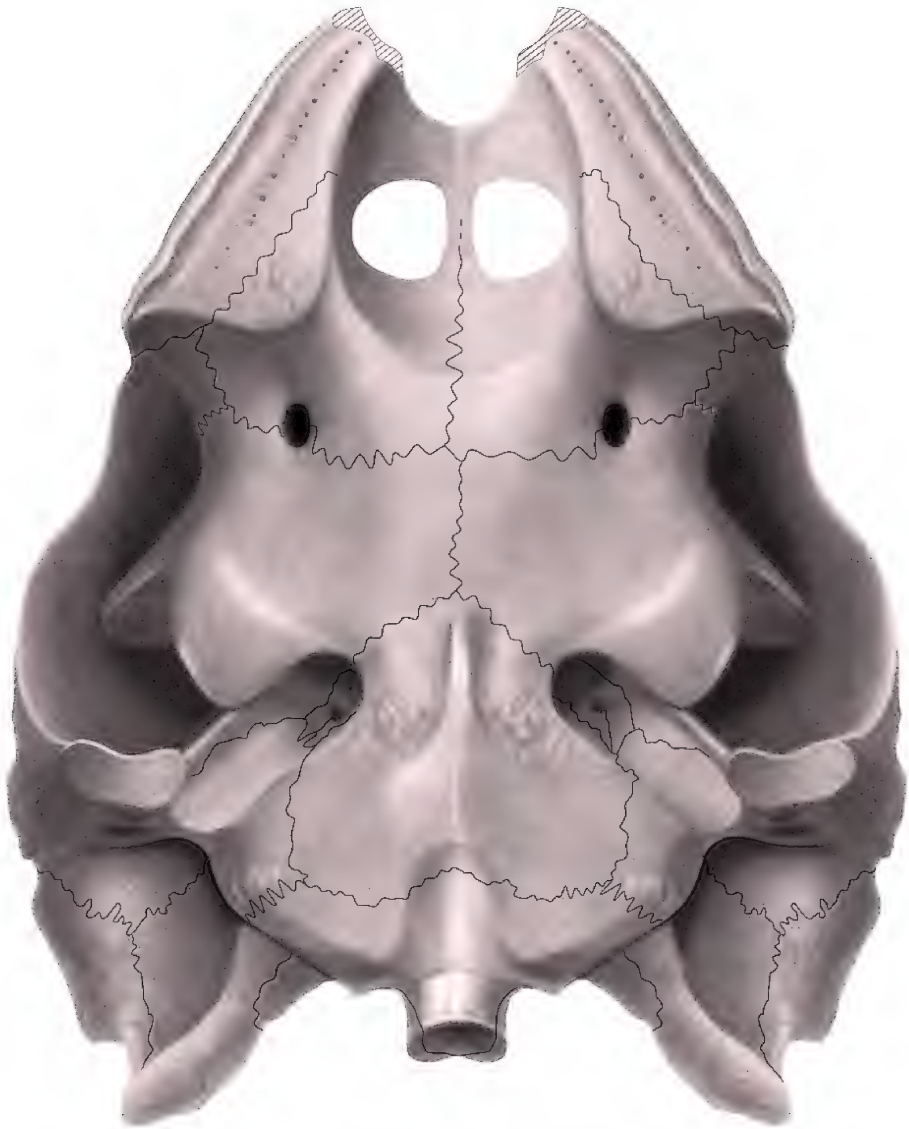


Fig. 2. *Hamadachelys escuilliei* Tong and Buffetaut, 1996. Partially restored ventral view based on MDE T03 and AMNH 30644. [A. Phillips, del.]

Cretaceous and Early Tertiary Pelomedusoides in having distinct surface sculpture of concentric rings, nuchal bone width equals length; six neurals (rarely seven) extending to costal seven; second neural always four sided; axillary buttress extending onto second costal and reaching to third peripheral anteriorly; suture for axillary buttress broad medially and narrow laterally; second costal thickened to support axillary buttress; bridge peripherals guttered dorsally; D-shaped iliac scar that does not cross from the eighth onto the seventh costal; internal gutter of posterior peripherals and pygal absent; gular scales usually not restricted to epiplastra; intergular scale narrow in contrast to bothremydids; short contact of humeral scales on midline; pectoral scales contact entoplastron and epiplastra, but do not contact mesoplastra.

### *Bauruemys elegans* (Suárez, 1969a)

*Podocnemis elegans* Suárez, 1969a
*Bauruemys elegans* (Suárez, 1969a) Kischlat, 1994

TYPE SPECIMEN: The number of the type specimen of this species is in some ambiguity, but we conclude with the assistance of our colleagues, G. Oliveira and P.S.R. Romano, that the type is MCT 1492-R, an associated shell and skull. The original author did not designate a holotype by number but he figured the shell, carapace, and plastron. However, the skull that was figured (Suárez, 1969a: figs. 6, 7) does not belong to the type specimen; it is MCT 1753-R (figs. 11, 12), and should be considered a paratype based on the text of Suárez (1969a; P.S.R. Romano, personal commun.). Candeiro et al. (2006: 927) confusingly state "holotype of *B. elegans* is UFRGS 148 and MN-V 4487, a postcranium...." Oliveira and Romano (2007) say (in translation) that although these specimens are representative of the species, they have concluded, following an extensive examination of the collections involved, that neither specimen should be referred to the type material of *B. elegans.* We agree that the type of *Podocnemis elegans* Suárez, 1969a, is MCT 1492-R, a skull (figs. 9, 10) and shell with scapulocoracoids, femur, and humerus. This identification is based on the shell figures in Suárez (1969a: figs. 2–4; 1969b: figs. 1–5).

The type skull, MCT 1492-R (figs. 9, 10), is dorsoventrally crushed and much of the bone is broken. The right side is better preserved than the left in general. The prefrontals are present but broken anteriorly. The frontals are both present with clear sutures. Both parietals are broken laterally and posteriorly. Portions of the jugal where it contacts the maxilla are present on both sides, but its posterior contacts are damaged or missing. Only small parts of the quadratojugals are identifiable, and the postorbitals are either missing (left) or broken and overlapped with the jugal and quadratojugal (right). Only a small portion of the anterior margins of the left squamosal are preserved and none of the right. The cheek emargination is partially preserved on the right side but badly damaged, and it is not determinable on the left side.

The premaxillae are represented only by a part of the horizontal plate visible in dorsal view. The left maxilla has the portion below the orbit preserved with the labial ridge intact, but its anterior portion is missing and its posterior margins broken. The right maxilla is more complete, but is covered ventrally by matrix, which helps hold it together along with some loose bone fragments on the ventral surface. The vomer is missing. The left palatine is cracked and missing its anterior margins but is otherwise intact. The right palatine is badly broken and represented only by the posteromedial piece.

The right quadrate is preserved medially, but the cavum tympani and processus articularis are gone. The left quadrate has a partially crushed and broken cavum tympani and the processus articularis present. The medial contacts of both quadrates are preserved. The left pterygoid is nearly complete except for some cracking and slight displacement. The right pterygoid lacks most of its lateral portion and is partially obscured by displaced bone fragments. On both sides, the cavum pterygoidei is preserved, although its margins are broken edges. The anteromedial part of the supraoccipital is preserved, but all of the crista supraoccipitalis is gone. Both exoccipitals are present but slightly broken along the margin of the foramen magnum, and the condylus occipitalis is broken off. The basioccipital is complete except for the condylus occipitalis. Both prootics are present and complete but mostly covered by matrix. The left opisthotic lacks some of its posterior process and the right one lacks all of it. The basisphenoid is complete, with clear sutures.

To the extent that it is preserved, the type skull agrees in detail with the other skulls ascribed to this species that are described below.

TYPE LOCALITY: "Tartaruguito" locality, near kilometer 736 of the old Sorocabana Railway branch, Pirapozinho, São Paulo State, Brazil, 22°13′08″S, 51°25′59″W (Romano and Azevedo, 2007; also see Bertini et al., 2006, for map; Oliveira and Romano, 2007). Suárez (2002), Henriques et al. (2005), Henriques (2006), Bertini et al. (2006), discuss the taphonomy and depositional history of this locality.

HORIZON: Adamantina Fm. fide Suárez (2002), Bertini et al. (2006).

DIAGNOSIS: As for genus.

REFERRED MATERIAL: MCT 1753-R, figured by Suárez (1969a: figs. 6, 7; 1969b:

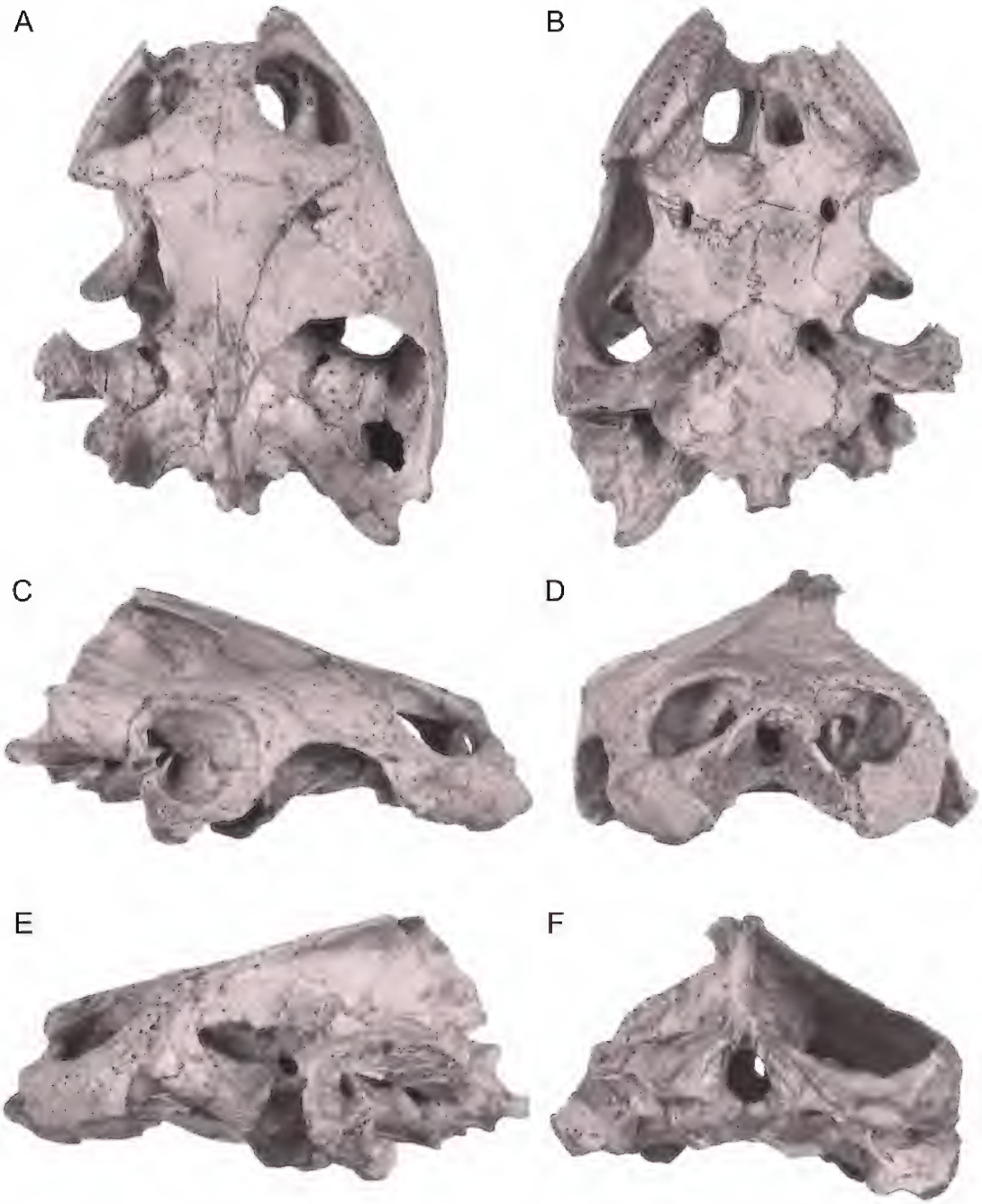



Fig. 3. *Hamadachelys escuilliei* Tong and Buffetaut, 1996. MDE T03. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [A. Phillips, del.]

figs. 5, 6), but not associated with type specimen. This skull (described below, figs. 11, 12) is the best preserved of the *Bauruemys* we have seen; all bones, except the vomer, are known from either one side or the other. The horizontal plates of the premaxillae are cracked and a few small pieces are missing. The crista supraoccipitalis

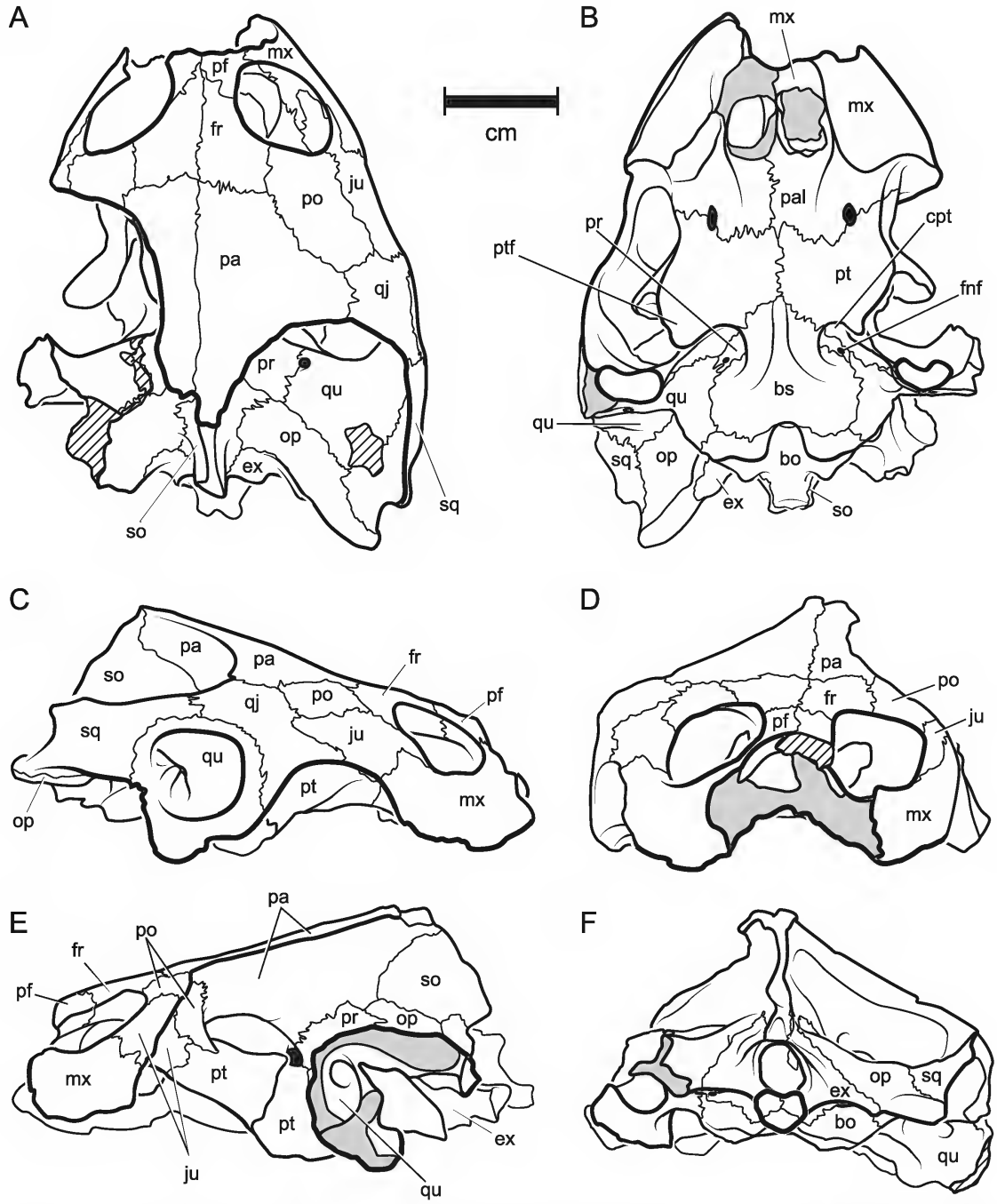



Fig. 4. *Hamadachelys escuilliei* Tong and Buffetaut, 1996. MDE T03. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [A. Phillips, del.]

is cracked and broken and has been repaired by reconstructing the available pieces. The result shows all the limits of the crista, but it is slightly deformed by crushing. Both temporal margins are dorsoventrally crushed but not collapsed, only depressed from the level of the skull roof. A small portion of the posteromedial part of the left parietal is

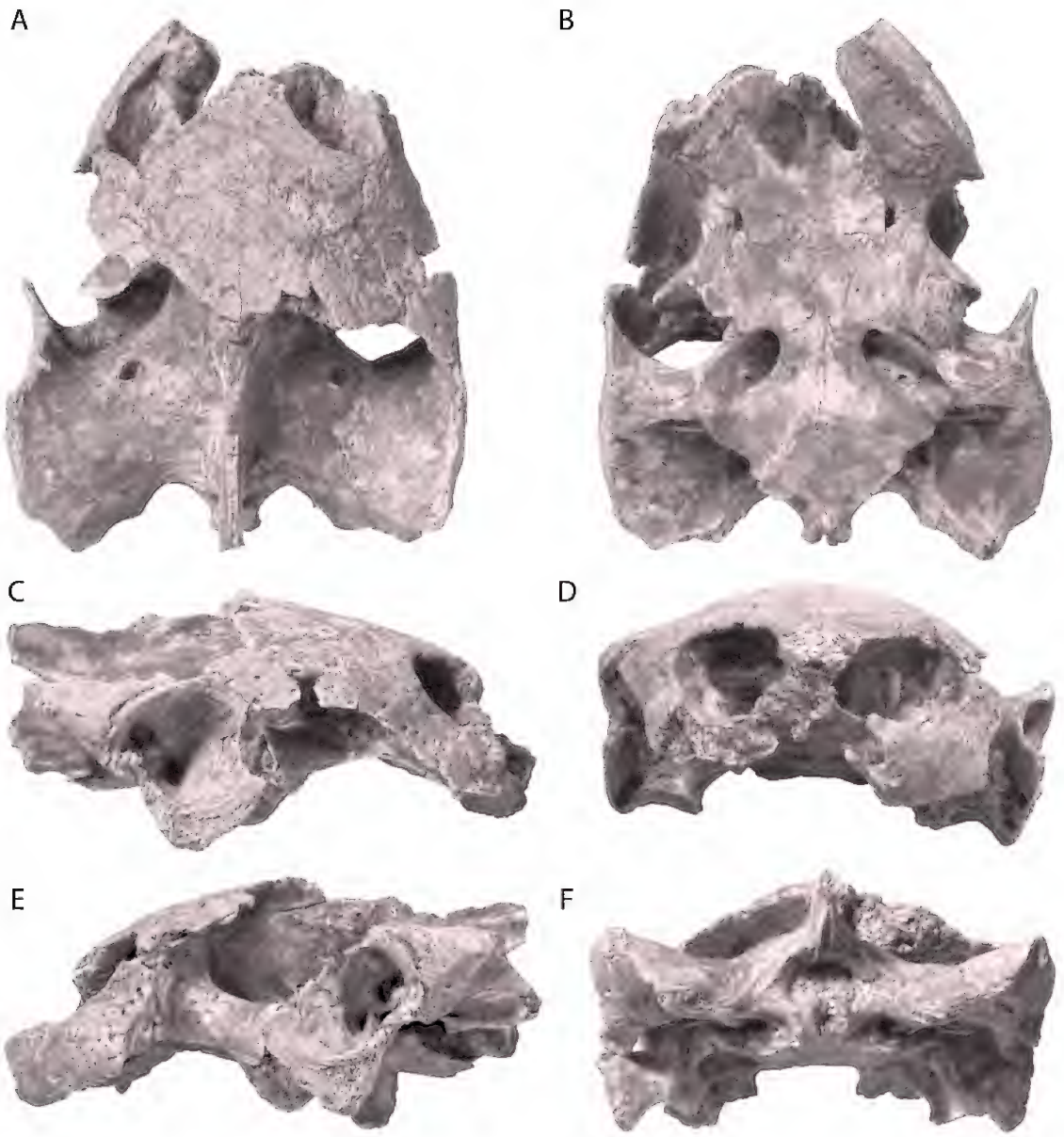



Fig. 5. *Hamadachelys escuilliei* Tong and Buffetaut, 1996. AMNH 30644. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [C. Facella del.]

missing. The posterior end of the right squamosal is missing. On the ventral surface, the pterygoid flanges are broken away and the floor of the cavum pterygoidei has been removed by preparation to expose the internal features of the cavum pterygoidei.

DGM uncataloged (collected 1969, Campos and Silva), carapace and plastron disarticulated with postcranial material in carapace part, including an eighth cervical vertebra.

MCZ 4123, a more complete skull than DGM uncataloged (above), but it is slightly more distorted and deformed by crushing (figs. 13, 14). MCZ 4123 has the vomer intact and the pterygoid flanges preserved on both sides. It is the only *Bauruemys* we have seen to have the flanges intact. The fossa nasalis

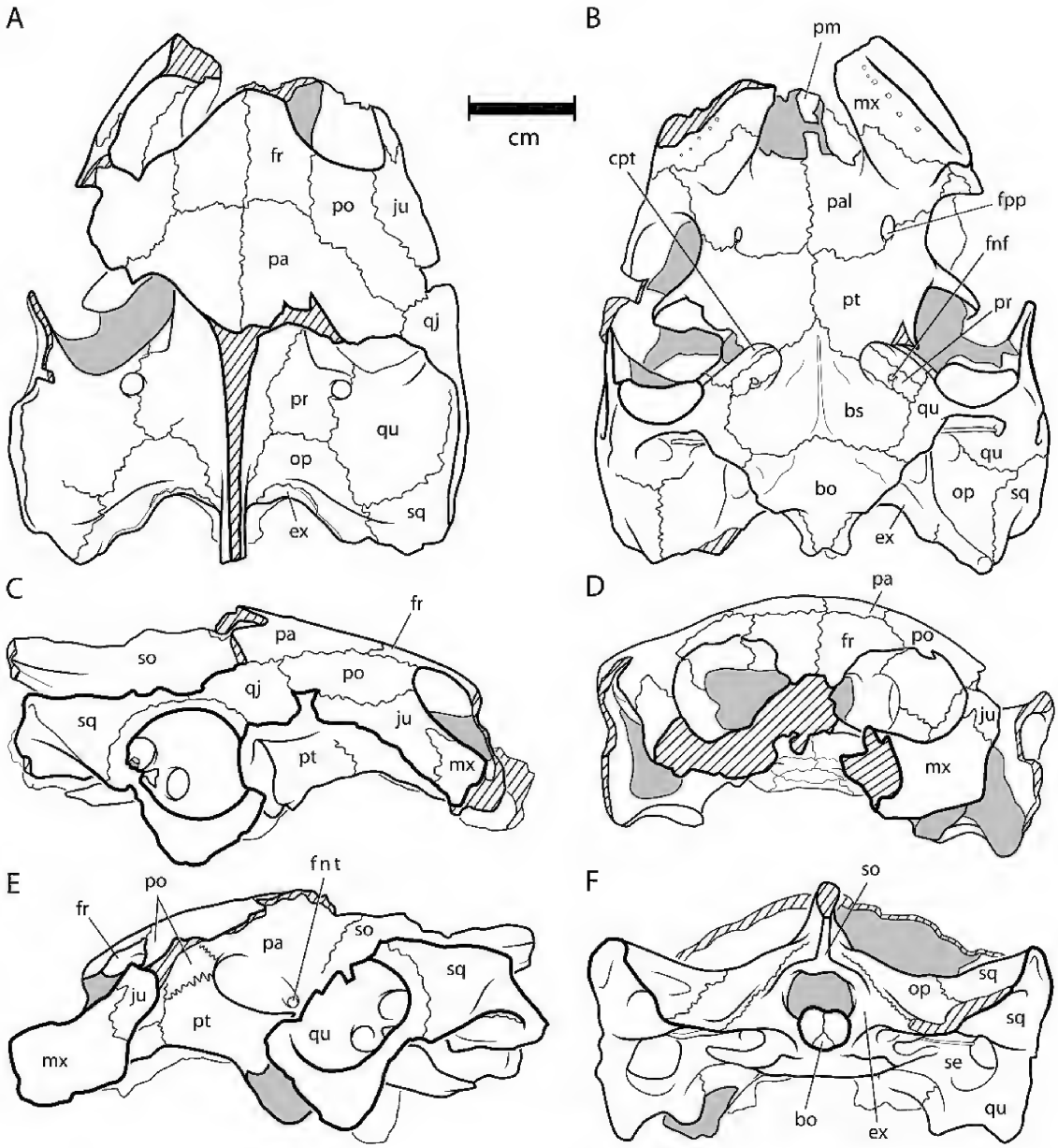



Fig. 6. *Hamadachelys escuilliei* Tong and Buffetaut, 1996. AMNH 30644. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [C. Facella del.]

has been deformed by lateromedial crushing, but the elements are all present and the only area lost is part of the horizontal plates of the premaxillae. The right prefrontal is crushed and displaced onto the frontal. As in DGM uncataloged, the posterior parts of the temporal roof have been pushed ventrally below the level of the skull roof, but the bones are missing only a few small pieces and the temporal margins are intact. Some missing areas of the parietals, left cheek, and supraoccipital have been filled in or repaired with resin.

AMNH 7888 consists of the skull, attached lower jaws, and attached fragments, including a centrum and phalange, to the

TABLE 1
**Comparison of Skulls of Mesozoic and Early Tertiary Podocnemididae**

| | *Hamadachelys* | *Bauruemys* | *Lapparentemys* | *Peiropemys* | *Pricemys* | *Podocnemis expansa* |
|---|---|---|---|---|---|---|
| Skull shape | narrow | wide | narrow, wide | narrow | narrow? | narrow |
| Interorbital groove | absent | absent | absent | absent | ? | present |
| Temporal emargination | more | more | less | less | less | less |
| PA-PT contact | absent | absent | absent | absent | ? | absent or present |
| Jugal size | smaller | smaller | smaller | smaller | smaller | larger |
| JU-PA contact | absent | absent | absent | absent | ? | present |
| PO size | larger | larger | larger | larger | ? | smaller |
| PO-QJ contact | present | present | present | present | ? | absent |
| Cheek emargination | less | less | more | more | more | less |
| Accessory ridge on triturating surface | absent | absent | absent | absent | absent | present |
| VO-MX contact | ? | narrow | wide | wide | ? | absent |
| Fossa precolumellaris | deep | deep | shallow | deep | shallow | shallow and moderate |
| Foramen jugulare posterius | open | open | closed | closed | closed | closed |
| BO-OP contact | very narrow | narrow | wide | wide | wide | wide |
| Tuberculum basiccipitale widely separated | no | no | yes | yes | yes | yes |
| Age | Cenomanian | Maastrichtian | Early Paleocene | ?Maastrichtian | ?Maastrichtian | Recent |

right of the crista supraoccipitalis. The skull is missing the vomer, both prefrontals, both frontals, anterior parts of the parietals, dorsal parts of the premaxillae, anterior parts of the maxillae, and some of the pterygoid flanges. Although the vomer is missing and the lower jaws are in place, the ventral surface of the premaxillae is well preserved and visible. The lower jaw is missing some pieces anteriorly.

AMNH 30643 consists of roughly the right half of a skull, showing the fossa orbitalis, the sulcus palatinopterygoideus, and the fossa temporalis. The right cheek, cavum tympani, crista supraoccipitalis, and temporal roof are missing. The occiput is damaged and it lacks the condylus occipitalis.

AMNH 30642 consists of roughly the left half of the skull without the snout region. The left otic chamber and cavum tympani are well preserved. The dorsal surface of the basicranium is exposed from the rostrum basisphenoidale anteriorly to the condylus occipitalis posteriorly, showing the area of the dorsum sellae and associated structures.

AMNH 30774, two partial lower right jaws and miscellaneous fragments associated with AMNH 30642 and AMNH 30643.

MN 4322-V, nearly complete skull, lacking the premaxillae, anterior parts of the maxillae, vomer, lateral parts of the pterygoids, and some of the occipital surfaces. The more internal areas are still encased in matrix.

MN 4323-V, partial skull, lacking the right quadrate, occipital surfaces, and much of the palate. It still has matrix on many of the surfaces.

MN 4324-V, posterior half of a skull, lacking everything anterior to the pterygoid-palatine suture. The center of the cavum cranii is exposed in the anterior surface of the break. The posterior temporal margin is preserved.

MN 4487-V, two cervical vertebrae referred to by Kischlat (1994: 348).

MCZ 4125, anterior half of a shell, with costals 1–4, neurals 1–4, anterior half of plastron with right mesoplastron. Only a few peripherals are preserved.

MCZ 4122, anterior margin of a shell, with the nuchal, peripherals 1–3, and the anterior plastral lobe.

MCZ 4127, right maxilla and palatine with ventral surfaces exposed.

MCZ 4128, partial skull lacking the prefrontals, frontals, postorbitals, and quadratojugals, left quadrate, on the dorsal surface. The posterior rami of the lower jaws are in place on the ventral surface. Most of the elements visible in ventral view are present, but are cracked and not well preserved.

MCZ 4129, partial skull consisting of the snout region exposed in ventral view and the otic chambers and cavum cranii exposed in a break.

MCZ 4124, small block of matrix with some limb elements in situ.

PREVIOUS WORK: Although Suárez (1969a) appears to be the legitimate publication for the type announcement for *Podocnemis elegans*, there are two other possible publications listed by Oliveira and Romano (2007) that contain a type announcement. One of these, not listed in our bibliography but listed in Oliveira and Romano (2007: 127), is a short paper that we interpret as an unpublished abstract, not a legitimate taxonomic description. The other, Suárez (1969b), has the same text and figures as Suárez (1969a) with a different page and figure arrangement, but exactly the same content. We do not know the relative dates of publication.

In addition to the generic name proposed in Kischlat (1994), Kischlat (1996a, 1996b), and Kischlat et al. (1994) provide other hypotheses about the relationships and geologic distribution of *Bauruemys*. Romano and Azevedo (2007) present a morphometric study of this species, possible due to the relatively large numbers of specimens available. They support the hypothesis of a single species in the sample studied.

DISCUSSION: Peirópolis B, the smaller of the two unnamed shell taxa from Peirópolis, is known only from isolated shell elements. It shares derived features with *Bauruemys elegans,* but is too poorly known to be referred to this species.

Kischlat (1994: 348) described two cervical vertebrae of *Bauruemys elegans* as lacking saddle-shaped or heterocoelous articulations (in the sense of Williams, 1950; Hoffstetter and Gasc, 1969). We have also examined these vertebrae and a number of similar cervicals in the uncataloged collections of the DNPM. The articulations are clearly similar to the cervical morphology of the outgroups, such as in *Euraxemys* and pelomedusids, in being a relatively simple, hemispherical, concave-convex articulation, not the more complex surface ("saddle-shaped") seen in *Podocnemis* and *Peltocephalus,* and not the wide, surface seen in *Turkanemys* and *Erymnochelys.*

Subfamily Podocnemidinae Cope, 1868

NEW DIAGNOSIS: Members of the Podocnemididae; quadratojugal-parietal contact long; foramen jugulare posterius closed; tuberculum basioccipitale widely spaced; crista supraoccipitalis with horizontal plate on ventral edge (except in *Erymnochelys* and *Peltocephalus*); cervical centra saddle shaped (except in *Erymnochelys* and *Turkanemys,* which have a third state).

INCLUDED TAXA: *Podocnemis* Wagler, 1830; *Peltocephalus* Duméril and Bibron, 1835; *Erymnochelys* Baur, 1888; *Bairdemys* Gaffney and Wood, 2002; *Dacquemys* Williams, 1954c; *Neochelys* Bergounioux, 1954; *Shweboemys* Swinton, 1939; *Stereogenys* Andrews, 1901; *Caninemys* Meylan, Gaffney, and Campos, 2009; *Turkanemys* Wood, 2003; *Neochelys* Bergounioux, 1954; *Papoulemys* Tong, 1998; *Peiropemys,* n. gen.; *Lapparentemys,* n. gen.; *Pricemys,* n. gen.; *Mogharemys,* n. gen.; *Cordichelys,* n. gen.; *Latentemys,* n. gen.; *Brontochelys,* n. gen.; *Albertwoodemys,* n. gen.; *Lemurchelys,* n. gen.

DISCUSSION: Two subfamilies of the Podocnemididae have been named by Broin (1988 [1989]) the "subfamily Podocnemidinae" and the "subfamily Erymnochelinae." Although used in a number of additional papers (Broin, 1991; Lapparent de Broin, 2000b, 2001, 2003a, 2003b), the most complete expression of the hypothesis is Lapparent de Broin (2000b).

The "subfamily Podocnemidinae" was considered by Lapparent de Broin (2000b) as containing *Podocnemis, Peltocephalus, Bauruemys,* "aff. *Roxochelys vilavilensis*" (= *Lapparentemys*), and *Stupendemys.* This

group of Lapparent de Broin (2000b) was not confirmed in our analysis. Besides the successive sister-group relationship of (*Bauruemys* (*Lapparentemys* (*Podocnemis*))), we have found a number of characters linking *Peltocephalus* with the taxon below, Lapparent de Broin's "Erymnochelyinae." In our analysis, the "subfamily Podocnemidinae" of Lapparent de Broin (2000b) is simply the South American podocnemidids. The character that seems to be dominant in Lapparent de Broin (2000b, and other papers) for this taxon is the saddle-shaped cervicals, but biogeography may have been an influential phylogenetic character. There is a series of shell characters as well, but the distributions are not clear. Apparently, the fact that *Bauruemys* lacks the cervical character was not yet known and the author used the shell features and geography to place this species in this group.

The "subfamily Erymnochelinae" was considered by Lapparent de Broin (2000b) as containing *Erymnochelys, Neochelys, Stereogenys, Shweboemys, Dacquemys,* and *"Carteremys"* (the last genus a nomen dubium in Gaffney et al., 2006). This group is essentially the present authors' magnatribe Erymnochelydand. The reflection of the cladogram in the classification requires its change in rank from Lapparent de Broin (2000b), but we agree in most of its content and its principal character. The primary character used for this group (Lapparent de Broin, 2000b: 70) is the "Much eroded roof of the enlarged carotid canal, the prootic and quadrate being so much eroded that the floor of the canalis cavernosus is broken and this canal is anteriorly confluent with the part of 'enlarged canal' leading to the sulcus cavernosus (not known in *Dacquemys*, homoplastic but with a less eroded roof in the podocnemidine *Peltocephalus*)." The interesting fact that the character does actually occur in a member of Lapparent de Broin (2000b)'s other subfamily (i.e., *Peltocephalus*) is recognized by Lapparent de Broin (2000b), but the geographic distribution was perhaps a more important consideration. There are now a few cervicals showing that extinct members of Lapparent de Broin's "Erymnochelyinae" did have saddle-shaped centra.

When analyzing only the Recent genera, none of the molecular results reproduce the Lapparent de Broin (2000b) resolution of (*Erymnochelys* (*Podocnemis, Peltocephalus*)); rather they prefer the (*Peltocephalus* (*Podocnemis, Erymnochelys*)) arrangement, while the present paper agrees with neither and finds the (*Podocnemis* (*Peltocephalus, Erymnochelys*)) resolution to be most attractive (see Phylogenetic Analysis).

Gaffney and Meylan (1988) used "Podocnemidinae Williams, 1954 (as 'podocnemides')" as an equivalent to what we now call the family Podocnemididae. In the present paper we redefine the subfamily Podocnemidinae to be the monophyletic group consisting of all Podocnemididae except *Bauruemys.*

### Infrafamily **Peiropemydodda,** new

DIAGNOSIS: Members of the subfamily Podocnemidinae; cheek emargination reaches above level of orbit; characters also found in *Bauruemys*: medial expansion of triturating surface absent; accessory ridges absent from the triturating surface.

DISTRIBUTION: Late Cretaceous of Brazil, Paleocene of Bolivia.

INCLUDED TAXA: *Peiropemys,* n. gen.; *Lapparentemys,* n. gen.; *Pricemys,* n. gen.

DISCUSSION: This grouping of three genera that are outside the common ancestor of the living species in our analysis really rests only on the combination of the smaller cheek emargination, as the absence of the medial expansion of the triturating surfaces with accessory ridges is primitive for the family. One step away from the shortest cladogram makes this group a multichotomy with *Podocnemis* and the magnatribe Erymnochelydand.

### ***Peiropemys,*** new genus

TYPE SPECIES: *Peiropemys mezzalirai,* new genus and new species.

INCLUDED SPECIES: *Peiropemys mezzalirai.*

DISTRIBUTION: Late Cretaceous, Brazil.

ETYMOLOGY: *Peiropos*, in allusion to the locality, Peirópolis; *emys*, Greek for "freshwater tortoise."

DIAGNOSIS: A podocnemidid known only from the skull; condylus occipitalis formed

only by exoccipitals uniquely among Podocnemididae (except for some *Peltocephalus*); skull relatively high and narrow in contrast to *Bauruemys*; orbits facing dorsolaterally; interorbital groove as found in *Podocnemis* absent; temporal emargination slight, in contrast to *Bauruemys* but greater than in *Peltocephalus*; postorbital large in contrast to *Podocnemis*; parietal-quadratojugal contact long; cheek emargination reaches above level of orbit; medial expansion of triturating surface, median maxillary ridge, absent, wide concavity on the midline, formed by the premaxillae and anterior maxilla present; accessory ridge on triturating surface absent; vomer present; vomer-maxilla contact wide; fossa precolumellaris deep as in *Bauruemys*; foramen jugulare posterius closed; interparietal scale equilateral triangle in contrast to parallel sided in *Pricemys*; cavum pterygoidei with small anterior opening for foramen cavernosum; horizontal occipital shelf present as in *Podocnemis*.

***Peiropemys mezzalirai,*** n. gen. et sp.

TYPE SPECIMEN: MCT 1497-R (figs. 15–18). This skull is a well-preserved and nearly complete specimen, lacking the right maxilla-jugal area and most of the premaxillae. The only parts unknown from one side or the other is the labial ridge area of the premaxilla, which is missing on both sides, and the distal edges of the pterygoid flange. The cavum cranii has been cleaned out, and the skull is free of most matrix. No crushing or distortion is visible.

TYPE LOCALITY: Caiera Quarry (of Campos and Kellner, 1999, and Kellner et al., 2005; same locality is "outcrop 1" of Carvalho et al., 2004, and Novas et al., 2008; "Point 1" of Ribeiro and Carvalho, 2007), at the southern end of the hill, Serra do Veadinha, near the old railroad station of Peirópolis, near the city of Uberaba (Municipality of Uberaba or Uberaba County), Minas Gerais State, Brazil. MCT 1497-R, type of *Peiropemys mezzalirai,* n. gen. et sp., was collected in 1959 by a team led by L.I. Price, DNPM, from the area excavated in that year as shown on the quarry map in Kellner et al. (2005: fig. 3).

Caiera Quarry, or Locality/Outcrop 1, has also yielded MCT 1498-R (the skull here named *Pricemys caiera,* n. gen. et sp.), MCT 1499-R (a large, nearly complete, shell of Peirópolis A), and many disarticulated turtle elements, here informally referred to as Peirópolis A and Peirópolis B.

According to Kellner et al. (2005), the original fossils from Caiera Quarry were found in 1947, with the main collecting efforts being in 1949, 1950, 1953, 1955, 1957, 1958, 1959, and 1961 (based on the published Caiera Quarry map in the DGM done under L.I. Price's direction, Kellner et al., 2005: fig. 3). Original discoveries apparently date back to 1945 when L.I. Price responded to reports of fossil discoveries made during the construction of a railway at Mangabeira, north of Uberaba (Ribeiro and Carvalho, 2007). During the time this quarry was in operation, a large number of fossils were collected, and over 185 square meters of the fossiliferous layer were exposed (Ribeiro and Carvalho, 2007: figs. 1, 2). Although the work at Caiera Quarry was apparently ended in 1961, there was later collecting around the base of the same hill, Serra do Veadinha, and in the same stratigraphic unit, Serra da Galga Member, Marília Fm., that held the initial quarry. D.A. Campos and L.I. Price in 1967 and 1969 collected turtles in this area, according to labeled specimens. Collections have continued to be made in this area and a paleontological museum has been built near the site (Ribeiro and Carvalho, 2007).

Other faunal elements from the Caiera Quarry include the prominent sauropods, but a frog, a lizard, crocodiles, and theropods, are also described or referenced in Carvalho et al. (2004), Kellner et al. (2005), Salgado and Carvalho (2008), Novas et al. (2008), and Candeiro (2009).

HORIZON: Serra da Galga Member, Marília Fm. (see Candeiro, 2009, and references).

DIAGNOSIS: As for genus.

ETYMOLOGY: For Sérgio Mezzalira, a DNPM geologist and invertebrate paleontologist who was very active in exploration and study of the Bauru Group and São Paulo State geology.

REFERRED MATERIAL: None. However, it is possible that the shell taxon informally referred to here as Peirópolis B belongs to *Peiropemys.* Peirópolis B is the smallest of the three shell taxa from this locality and the

one for which there is the most limited amount of material. The material is all disarticulated (figs. 92, 93, 95, 97), but some of it is associated. At present we have the nuchal, costals 1, 5, 7, and 8, peripherals 1 and 8–11, the suprapygal, and pygal. We cannot assign any plastron material to this taxon at this time, although, based on size and a different morphology than in Peirópolis A, we speculate that some of the smaller plastral elements may belong to this species. *Cambaremys langertoni*, found near the Caiera Quarry, is apparently a juvenile (França and Langer, 2005; Romano et al., 2009), and its small size may not be characteristic of the species. As far as we know at present, although the type and only known specimen of *Cambaremys langertoni* was found near the Caiera Quarry, only two taxa of turtles definitely occur in the quarry site. These are *Peiropemys* and *Pricemys*, based on skulls, and Peirópolis A and Peirópolis B, based on shells.

PREVIOUS WORK: Possibly the material referred to in Broin (1991: 515).

DISCUSSION: *Peiropemys* is the sister group to *Pricemys* + *Lapparentemys* in our analysis. These three genera are the sister taxon to all other podocnemidids, except *Bauruemys,* which is outside (*Peiropemys* (*Pricemys, Lapparentemys*)) and is the sister taxon to all podocnemidids. The morphology of these four genera and the Recent *Podocnemis* has "remained in all particulars in a pristine and unmodified condition (at least as regards their structure) through a grievous long period of time on Earth..." (Tedwelle in Gaffney, 1979: 69).

### ***Lapparentemys,*** new genus

SYNONYMY: ?*Roxochelys vilavilensis* Broin, 1971.

TYPE SPECIES: ?*Roxochelys vilavilensis* Broin, 1971.

INCLUDED SPECIES: *Lapparentemys vilavilensis* (Broin, 1971).

DISTRIBUTION: Paleocene of Bolivia.

ETYMOLOGY: Restudy of the type and two additional specimens of *Roxochelys wanderleyi* indicate that the species *vilavilensis* Broin, 1971, is not referable to the genus *Roxochelys*. Thus, we erect a new generic name, *Lapparentemys*, in honor of the many important contributions of France de Lapparent de Broin to our understanding not only of pleurodires, but of all turtles.

REVISED DIAGNOSIS: A podocnemidid known from the skull and postcrania; pectoral scales contact mesoplastra uniquely among Podocnemididae; skull relatively high and narrow in contrast to *Bauruemys*; orbits facing dorsolaterally; interorbital groove as found in *Podocnemis* absent; temporal emargination slight in contrast to *Bauruemys* but deeper than in *Peltocephalus*; postorbital large in contrast to *Podocnemis*; parietal-quadratojugal contact long; cheek emargination reaches above level of orbit; medial expansion of triturating surface, median maxillary ridge, absent; wide concavity on the midline, formed by the premaxillae and anterior maxilla, present; accessory ridge in triturating surface absent; vomer present; vomer-maxilla contact wide; fossa precolumellaris shallow as in *Podocnemis expansa*; foramen jugulare posterius closed; interparietal scale equilateral triangle; cavum pterygoidei with small anterior opening for foramen cavernosum; horizontal occipital shelf present as in *Podocnemis*; chorda tympani not enclosed in processus retroarticularis; nuchal bone width greater than length; seven neurals extending to costal seven.

The shell of this medium-size Pelomedusoides pleurodire (to 400 mm straight carapace length) differs from other South American Cretaceous and early Tertiary Pelomedusoides in having a relatively thick, elongate shell with deep scute sulci but no distinct surface sculpture; vertebral scales are narrow and parallel sided; a relatively short, wide nuchal bone is narrow anteriorly; first neural four sided; axillary buttress not extending onto second costal, reaching to third peripheral anteriorly; suture for axillary buttress broad and curving with parallel sides; second costal not thickened to support axillary buttress; bridge peripherals weakly guttered dorsally; iliac scar with anterior margin concave and crossing from the eighth onto the seventh costal both medially and laterally; internal gutter of posterior peripherals and pygal absent; gular scales restricted to epiplastra; intergular narrow; short humeral contact on midline; pectoral scales

contact epiplastron and entoplastron; pectoral scale contact to mesoplastron variable.

***Lapparantemys*** *vilavilensis* (Broin, 1971), new combination

?*Roxochelys vilavilensis* Broin, 1971

TYPE SPECIMEN: MNHNP VIL 1 (Broin, 1971: pl. 31, figs. 1, 2), a complete carapace and plastron.

TYPE LOCALITY: 2 kms south of Vilavila, later designated Villa Viscarra, Cochabamba Province, Bolivia.

HORIZON: Originally (Broin, 1971: 445) described from the late Cretaceous El Molino Formation, the horizon was later (Muizon et al., 1983; Broin, 1991) identified as the early Paleocene Santa Lucía Fm.

DIAGNOSIS: As for genus.

ETYMOLOGY: Named for the type locality near Vilavila (Broin, 1971: 445).

REFERRED MATERIAL: Specimens from the type locality listed in the hypodigm (Broin, 1991) include: MNHNP VIL 2, partial shell; MNHNP VIL 3, plastron; MNHNP VIL 4, partial plastron; MNHNP VIL 5, juvenile shell; MHNC 6902, partial shell; MHNC 6903, plastron.

AMNH 14444, a well-preserved and nearly complete skull (figs. 21, 22), lacking the distal end of the crista supraoccipitalis and the edges of the pterygoid flange. The skull is slightly distorted by dorsolateral compression from the right side, ventromedial compression from the left side. The fossa temporalis on both sides is free of matrix, but the cavum cranii is not. The lower jaw is present and is complete except for the right articular region. A small portion of the carapace is associated with the skull and it agrees with the other *Lapparentemys* shells. Locality and Horizon: "El Molino, Vila vila" (label).

WUS 2160, a complete shell (fig. 90) with skull (figs. 23–25) lacking the right skull roof and cheek. Before preparation the skull was articulated to the shell by the cervical vertebrae. The left premaxilla lacks its medialmost portions and the right one is mostly missing. The right maxilla lacks its labial ridge and the area below the orbital margin. The pterygoid flanges are broken, the right one is missing, and the left one is nearly all present. Only the anteroventral portion of the crista supraoccipitalis remains, the rest is missing. The lower jaws are present and nearly complete; only part of the left prearticular is missing. Locality and horizon: Santa Lucía Fm., Cochabamba Department, Bolivia, purchased George Helsp Fossils, 1994 (label).

RM 20.5155, skull, shell (fig. 89), cervicals, and limb bones in partial articulation. Specimen poorly preserved due to small cracks and displacements throughout. Locality and horizon: "Santa-Lucia, Tiupampa (label)," collector, Pierre-Yves Gagnier.

PREVIOUS WORK: Both Broin (1971) and (1991) provide important descriptions and figures of skulls and shells of this taxon. Numerous papers have referred to this taxon but provided no additional information.

DISCUSSION: We refer two additional specimens to *Roxochelys wanderleyi* (following Romano et al., 2009; see discussion below) greatly expanding our knowledge of the shell. As a result of this redescription based on new shell material of *R. wanderleyi,* the type species of *Roxochelys*, it is apparent that "?*Roxochelys vilavilensis*" Broin, 1971, cannot be referred to *Roxochelys*. Therefore, we have created a new genus, *Lapparentemys*.

*Lapparentemys* and *Pricemys* are linked by the possession of a shallow fossa precolumellaris.

Our examination of MNHNP material identified by Broin (1971, 1991) as "?*Roxochelys vilavilensis,*" leads us to believe that there may be more than one taxon in the original hypodigm and subsequently assigned specimens. In order to avoid possible problems of overlapping species, we have restricted our concept of *vilavilensis* to the holotype and other specimens listed above. We consider MNHNP VIL-6 and MHNC 6904 to represent two possible, additional unnamed taxa that are excluded from our concept of *Lapparentemys vilavilensis*.

MNHN VIL-6 is a small round carapace with an associated plastron (Broin, 1991: pl. I, figs. 1–4). It has a very different overall shell shape than the type of *vilavilensis* or other specimens with skulls referable to *vilavilensis*. In our opinion the small size is not due to immaturity as all sutures are closed and the shell is well ossified. In MNHNP VIL-6 the pleuro-marginal sulci

are on the costoperipheral sutures, which is not the case in the type of *vilavilensis* or other specimens with skulls that are referable to *vilavilensis*. The epiplastron differs in having a long straight anterior margin and a more transverse posterior margin. Where the posterior margin of the epiplastron articulates with the hyoplastron it is straight and without a major posterior projection that can be seen in MNHNP VIL-3, which was collected with the *vilavilensis* type specimen. Furthermore, on the ventral surface, the pectoral scales reach the epiplastral suture, but do not cross onto the epiplastron as in *vilavilensis*. The vertebral scales in MNHNP VIL-6 are shorter and somewhat more hexagonal than in *Lapparentemys vilavilensis*.

MNHC 6904 is a specimen from Tiupampa (Broin, 1991: pl. II, figs. 8–11). It has a longer, narrower shell more similar to *vilavilensis* in overall form, but differs from *vilavilensis* in having a robust axillary buttress located on the posterior part of the first costal and producing some thickening of the second costal. The epiplastron has the same basic shape as *vilavilensis* but the pectoral scale appears to not reach the epiplastron as it does in material of *vilavilensis*. Unlike *vilavilensis*, the vertebrals of this specimen are more hexagonal. Resolution of the phylogenetic position of MNHN VIL-6 and MNHC 6904 is beyond the scope of this study. They are discussed to stress that they are not used in our concept of *Lapparentemys vilavilensis*.

### *Pricemys,* new genus

TYPE SPECIES: *Pricemys caiera,* new genus and species.

INCLUDED SPECIES: *Pricemys caiera,* new genus and species.

DISTRIBUTION: Late Cretaceous, Brazil.

ETYMOLOGY: For Llewellyn I. Price, influential Brazilian paleontologist and leader of the team that collected the type specimen and the other Caiera Quarry, Peirópolis, turtles.

DIAGNOSIS: A podocnemidid known only from the skull; skull relatively high and narrow in contrast to *Bauruemys*; interorbital groove as found in *Podocnemis* absent; temporal emargination slight in contrast to *Bauruemys* but deeper than in *Peltocephalus;* postorbital large in contrast to *Podocnemis*; parietal-quadratojugal contact long; cheek emargination reaches above level of orbit; medial expansion of triturating surface, median maxillary ridge, absent; wide concavity on the midline, formed by the premaxillae and anterior maxilla, present; accessory ridge in triturating surface absent; vomer present; fossa precolumellaris shallow as in *Podocnemis expansa*; foramen jugulare posterius closed; interparietal scale parallel sided in contrast to equilateral triangle in *Peiropemys*; cavum pterygoidei with small anterior opening for foramen cavernosum; horizontal occipital shelf present as in *Podocnemis*.

### *Pricemys caiera,* n. gen. et sp.

TYPE SPECIMEN: MCT 1498-R, a braincase (figs. 28, 29), left quadrate-squamosal (figs. 32, 33), and right maxilla-jugal (figs. 30, 31). The quadrate piece articulates with the braincase but the maxilla piece has no contacts with the rest of the skull. The braincase consists of the right quadrate, the medial part of the right squamosal, both prootics, both opisthotics (the left one is incomplete posteriorly), the supraoccipital, and most of both parietals. The lateral edges of both parietals, however, are incomplete. The right one is separated from the quadrate by matrix, but the left one shows the posterior part of the quadratojugal contact when articulated with the left quadratojugal-squamosal piece. MCT 1498-R preserves both exoccipitals, the basioccipital, and the basisphenoid. The pterygoids are present but lacking their anterolateral areas, the processus trochlearis pterygoidei and pterygoid flange in particular, but also the palatine contact. This specimen has been prepared with only the matrix supporting the remaining portions of skull roof. The internal structures of the cavum cranii, cavum acustico-jugulare, cavum acusticum, and cavum pterygoidei, are all visible and well preserved. The left stapes is preserved in situ.

The left quadrate-squamosal piece (figs. 32, 33) of MCT 1498-R preserves nearly all of the squamosal. The quadrate is complete in the area of the cavum tympani, but its medial contacts with the braincase piece have been lost. The skull appears to have been

slightly damaged by dorsoventral compression, although not deformed just broken along the parietal and quadrate contact areas. A fragment of stapes remains in the incisura columellae auris.

The right maxilla-jugal piece of MCT 1498-R (figs. 30, 31) preserves the maxilla from the premaxilla contact to the jugal. The labial ridge is broken except for a short section under the orbit, which gives the depth of the ridge. The dorsal process of the maxilla appears to end at the prefrontal contact. The lateral section of the palatine is also preserved where it forms part of the triturating surface and enters the floor of the fossa orbitalis. The jugal is preserved anteriorly, but its dorsal and posterior margins are broken edges. The anteroventral margin is natural and shows the depth of the cheek emargination.

TYPE LOCALITY: Caiera Quarry, near village of Peirópolis, near city of Uberaba, Minas Gerais State, Brazil. Collected in 1958 from base of Serra do Veadinha that yielded *Peiropemys* and MCT 1499-R, a large, nearly complete, shell in DNPM. See locality discussion under *Peiropemys mezzalirai,* n. gen. et sp., for more information.

HORIZON: Serra da Galga Member, Marília Fm. (see Candeiro, 2009, and references).

DIAGNOSIS: As for genus.

ETYMOLOGY: For locality of Caiera, near village of Peirópolis, near city of Uberaba, Minas Gerais, Brazil.

REFERRED MATERIAL: It is likely that an uncataloged DGM dentary (fig. 34) belongs to this species, as it fits well into, and is the same size as, the MCT 1498-R maxilla-jugal piece.

It is possible that the shell taxon referred to here as Peirópolis A (see Shell Morphology below) belongs to *Pricemys.* Peirópolis A is represented by a large number of disarticulated shell bones (figs. 91–93, 95–97), mostly complete single bones but not associated or articulated with others, collected mostly during the DNPM expeditions of 1949, 1950, 1953, 1955, 1957, 1958, 1959, and 1961. Included with these are three articulated specimens: (a) DGM Peirópolis 321, a complete plastron, at least some carapace, and some cervical parts, all disarticulated. The plastron of 321 is in a drawer labeled: "Desmonte 1967 Peirópolis Mun. Uberaba"; (b) MCT 1499-R (fig. 91B), a large shell with most of the carapace, the plastron, pelvis, and first thoracic present. From Peirópolis, Caiera Quarry, locality #1, the classic Peirópolis locality at lime plant, Bauru Fm., it is prepared with the plastron side up, the carapace is unprepared, and some of the anterior lobe is separate; (c) another Peirópolis shell, collected by Langerton, has a thickened dorsal lip of the epiplastra, which appears to be characteristic of Peirópolis A.

PREVIOUS WORK: Probably referred to in Broin (1991: 515).

DISCUSSION: Our resolution of this species is (*Peiropemys* (*Pricemys, Lapparentemys*)). It differs from its contemporary in the Caiera Quarry, *Peiropemys*, in a series of characters listed in table 2.

### Infrafamily Podocnemidodda Cope, 1868, new rank

DIAGNOSIS: Members of the subfamily Podocnemidinae; medial expansion of triturating surface with median maxillary ridge; accessory ridges present.

INCLUDED TAXA: *Podocnemis* Wagler, 1830; *Peltocephalus* Duméril and Bibron, 1835; *Erymnochelys* Baur, 1888; *Bairdemys* Gaffney and Wood, 2002; *Dacquemys* Williams, 1954c; *Neochelys* Bergounioux, 1954; *Shweboemys* Swinton, 1939; *Stereogenys* Andrews, 1901; *Caninemys* Meylan, Gaffney, and Campos, 2009; *Turkanemys* Wood, 2003; *Neochelys* Bergounioux, 1954; *Papoulemys* Tong, 1998; *Mogharemys,* n. gen.; *Cordichelys,* n. gen.; *Latentemys,* n. gen.; *Brontochelys,* n. gen.; *Albertwoodemys,* n. gen.; *Lemurchelys,* n. gen.

### Magnatribe Podocnemidand Cope, 1868, new rank

DIAGNOSIS: Same as for *Podocnemis.*

INCLUDED TAXA: *Podocnemis* Wagler, 1830.

DISCUSSION: The category magnatribe is created here to reflect the cladogram. We use the Latinized ending *-and.*

### *Podocnemis* Wagler, 1830

TYPE SPECIES: *Emys expansa* Schweigger (1812).

TABLE 2
**Comparison of Peirópolis Skulls (measurements in mm)**

| | *Pricemys caiera* MCT 1498 R | *Peiropemys mezzalirai* MCT 1497 R |
|---|---|---|
| Width at condylus mandibularis | 98.0 | 79.0 |
| Width | 124% | 100% |
| Height at condylus occipitalis | 43.8 | 38.5 |
| Height ratio | 113% | 100% |
| Triturating surface | slightly wider | slightly narrower |
| Low convexity on triturating surface | present | absent |
| Condylus occipitalis | equal parts of EX and BO | BO very small, EX large |
| Antrum postoticum | smaller | larger |
| Fossa precolumellaris | shallow | deep |
| Scale on parietals | parallel sided, extends to edge of roof | triangular, widely separated from roof margin by other scales meeting |

INCLUDED SPECIES: *Podocnemis expansa, P. vogli, P. unifilis, P. erythrocephala, P. lewyana, P. sextuberculata, P. bassleri.*

DISTRIBUTION: Northern South America.

DIAGNOSIS: A podocnemidid with postorbital small allowing jugal-parietal contact; jugal unusually large; interorbital groove present, uniquely among Podocnemididae; skull relatively high and narrow in contrast to *Bauruemys*; orbits facing dorsolaterally; temporal emargination slight in contrast to *Bauruemys* but deeper than in *Peltocephalus*; parietal-quadratojugal contact long; cheek emargination reaches level of orbit; medial expansion of triturating surface, median maxillary ridge, present; accessory ridge or ridges present in triturating surface; vomer absent (except in *P. vogli*); fossa precolumellaris varying from shallow to moderate but not as deep as in *Bauruemys*; foramen jugulare posterius closed; interparietal scale equilateral triangle or elongate triangle; cavum pterygoidei with small to moderate anterior opening for foramen cavernosum; horizontal occipital shelf present as in *Peiropemys*; chorda tympani not enclosed in processus retroarticularis.

Postcrania with cervical centra saddle shaped; nuchal bone width greater than length; seven neurals extending to costal eight; axillary musk duct absent from buttress (except in *P. erythrocephala*), axillary buttress reaching second peripheral (except in *P. vogli*), pectoral scales do not contact mesoplastra, but do contact entoplastron and epiplastra.

PREVIOUS WORK: Baur (1890) gave a comparative diagnosis for *Podocnemis, Peltocephalus,* and *Erymnochelys* (repeated under *Erymnochelys* discussion), when he authored *Erymnochelys*. Boulenger (1889) gives a diagnosis for *Podocnemis* sensu lato, synonymizing *Peltocephalus* and *Erymnochelys,* for the Recent species of the family as currently constituted. The same is true for Siebenrock (1902), Williams (1954a), and Wermuth and Mertens (1961, 1977). The Pritchard and Trebbau (1984) diagnosis was published after the separation of the three genera was widely accepted. All of these emphasize characters visible in the preserved whole animal with limited if any osteologic characters. Although there is no systematic information, Groombridge (1982) has references for biology of the various living species. Fritz and Havas (2007) and Bickham et al. (2007) are the most recent to produce species lists and synonymies of variable usefulness.

DISCUSSION: We follow Iverson (1992) who, in turn, followed Williams (1954a) and Pritchard and Trebbau (1984), in the recognition of six living species of *Podocnemis* sensu stricto. See all three references for an introduction to the literature on this genus. As our present work is not primarily concerned with these species, we do not review this literature. The specimens listed below as Referred Material are only a few of the ones we have actually seen and do not reflect the material available in collections or referred to in the literature.

Although there have been few suggestions of relationships among the living *Podocnemis* species, Mittermeier and Wilson (1974) argued that *erythrocephala, unifilis, lewyana, vogli,* form a monophyletic group within *Podocnemis.* They called this the "vomerine

group" (ibid.: 157), based on the possession of at least two parallel ridges on the triturating surface (three in *vogli*, which they interpreted as primitive) and elongate heads. Frair et al. (1978) produced a resolution of: (*P. expansa, P. vogli, P. lewyana, P. unifilis, P. erythrocephala* (*P. sextuberculata*)), based on a serological analysis. Cadena et al. (2010) did not resolve these species.

Our resolution of these species is: (*P. vogli* (*P. lewyana* (*P. unifilis* (*P. erythrocephala* (*P. sextuberculata, P. expansa*))))). There is virtually nothing in common with this resolution and the molecular study of Vargas-Ramírez et al. (2008). Most of the characters we have used that actually resolve these species are frequently subject to homoplasy in other turtle taxa, and are reversed within our own study, so we do not consider this part of the analysis to be strongly supported as the resolution collapses into a multichotomy at one step more than the shortest resolution (fig. 98). Osteologically, these Recent species are very similar to each other and have relatively conservative morphologies even within a group that has changed little since the late Cretaceous.

In our resolution of the character list presented here, the following characters are unique synapomorphies for *Podocnemis*: interorbital groove, jugal-parietal contact, postorbital smaller than orbit (except in *P. unifilis*), and foramen nervi abducentis large (also in *Pricemys*, and not determinable in many fossil skulls).

For the living species of *Podocnemis*, our analysis produces the following characters (see also Character List under Conclusions) supporting the resolution in fig. 98:

*(P. expansa, P. sextuberculata)* – character 6, parietal and pterygoid contact in septum orbitotemporale present and narrow; character 30, fossa precolumellaris present but shallow.

*((P. expansa, P. sextuberculata) P. erythrocephala)* – character 36, anterior opening of cavum pterygoidei moderate in size.

*(((P. expansa, P. sextuberculata) P. erythrocephala) P. unifilis)* – character 70, axillary musk duct with three openings.

*((((P. expansa, P. sextuberculata) P. erythrocephala) P. unifilis) P. lewyana)* – character 8, interparietal scale elongate triangle; character 22, vomer absent; character 68, axillary buttress reaches peripheral two.

*(((((P. expansa, P. sextuberculata) P. erythrocephala) P. unifilis) P. lewyana) P. vogli)* – characters for genus *Podocnemis* listed above.

### *Podocnemis expansa* (Schweigger, 1812)

SYNONYMY: See Boulenger (1889), Siebenrock (1902, 1904), Wermuth and Mertens (1961, 1977), Pritchard and Trebbau (1984), and Iverson (1992).

TYPE SPECIMEN AND LOCALITY: See Iverson (1992).

DIAGNOSIS: See Boulenger (1889), Siebenrock (1902), Williams (1954a), Pritchard and Trebbau (1984).

REFERRED MATERIAL: YPM Herpetology 15401, AMNH Herpetology 58098, AMNH Herpetology 62947, NMV 1852, USNM 222470, YPM Herpetology 204, FMNH Herpetology 98958 (49), USNM Herpetology 65112, USNM Herpetology 65113, USNM Herpetology 28976, USNM Herpetology 28975.

PREVIOUS WORK: Siebenrock (1902) and Williams (1954a) provide useful information. Groombridge (1982) and Valenzuela (2001) have general literature reviews. Williams (1950; redrawn in Hoffstetter and Gasc, 1969) figures the cervical vertebrae. Williams (1954a) figures the palate. Good skull figures are in Grey (1855, repeated in Gaffney, 1979) and Hay (1908). Gaffney (1990) figures most of the postcranial osteology except the shell. Pritchard and Trebbau (1984) figure skull and shell with sutures.

DISCUSSION: Although relatively common in collections and referred to in many systematic works, there is no rigorous, comparative morphologic diagnosis for this species (or the genus *Podocnemis* for that matter). Among the references indicated, Williams (1954a) and Pritchard and Trebbau (1984) do provide descriptive information particularly useful in preserved specimens but few comparative osteologic characters.

### *Podocnemis vogli* Müller, 1935

SYNONYMY: See Wermuth and Mertens (1961, 1977), Pritchard and Trebbau (1984), Iverson (1992).

TYPE SPECIMEN AND LOCALITY: See Iverson (1992).

DIAGNOSIS: See Williams (1954a) and Pritchard and Trebbau (1984).

REFERRED MATERIAL: UF 39100, MCZ 53626, USNM Herpetology 266206.

PREVIOUS WORK: Müller (1935) has figures of skulls in dorsal and ventral views, shells figured without sutures. Pardo (1969) has figures of cranial as well as shell scales. Williams (1954a) figures the palate. Pritchard and Trebbau (1984) figure the skull and shell with sutures, and review the literature. Groombridge (1982) has a general review of the literature. We have included new figures of the skull of *Podocnemis vogli* for comparison (figs. 35, 36).

### *Podocnemis lewyana* Duméril, 1852

SYNONYMY: See Siebenrock (1902), Boulenger (1889), Wermuth and Mertens (1961, 1977), Pritchard and Trebbau (1984: table 3), Iverson (1992).

TYPE SPECIMEN AND LOCALITY: See Iverson (1992).

DIAGNOSIS: Boulenger (1889), Siebenrock (1902) and Williams (1954a) have some comparative information, but there is no thorough comparative diagnosis for this species.

REFERRED MATERIAL: FMNH 73790, MCZ 53281, DGM 283RR, USNM Herpetology 108580.

PREVIOUS WORK: Siebenrock (1902) and Williams (1954a) provide useful information. Williams (1954a) figures the palate. Groombridge (1982) has a general literature review.

### *Podocnemis sextuberculata* Cornalia, 1849

SYNONYMY: See Boulenger (1889), Siebenrock (1902), Wermuth and Mertens (1961, 1977), Pritchard and Trebbau (1984: table 3), Iverson (1992).

TYPE SPECIMEN AND LOCALITY: See Iverson (1992).

DIAGNOSIS: Siebenrock (1902) and Williams (1954a) have some comparative information, but there is no thorough comparative diagnosis for this species.

REFERRED MATERIAL: USNM 65109, USNM Herpetology 65110, USNM Herpetology 65111, USNM Herpetology 51979, AMNH Herpetology 58108, FMNH Herpetology 16075.

PREVIOUS WORK: Boulenger (1889), Siebenrock (1902) and Williams (1954a) provide useful information. Williams (1954a) figures the palate. Groombridge (1982) has a general literature review. We have included new figures of the skull of *Podocnemis sextuberculata* for comparison (figs. 37, 38).

### *Podocnemis unifilis* Troschel, 1848

SYNONYMY: See Boulenger (1889), Siebenrock (1902, 1904), Wermuth and Mertens (1961, 1977), Pritchard and Trebbau (1984), Iverson (1992), Mittermeier and Wilson (1974).

TYPE SPECIMEN AND LOCALITY: See Iverson (1992).

DIAGNOSIS: See Siebenrock (1902), Williams (1954a) and Pritchard and Trebbau (1984).

REFERRED MATERIAL: AMNH Herpetology 58200, NMV 1824, AMNH Herpetology 58104, AMNH Herpetology 58198, FMNH Herpetology 98865, FMNH Herpetology 98926, FMNH Herpetology 45657, FMNH Herpetology 211758, USNM Herpetology 313861.

PREVIOUS WORK: Boulenger (1889), Siebenrock (1902, 1904), Williams (1954a) provide useful information. Siebenrock (1904) has descriptions of the whole animal with figures; Pritchard and Trebbau (1984) figure skull and shell with sutures. Williams (1954a) figures the palate. Groombridge (1982) has a general literature review.

DISCUSSION: Although relatively common in collections and referred to in many systematic works, there is no rigorous, comparative morphologic diagnosis for this species. We have included new figures of the skull of *Podocnemis unifilis* for comparison (figs. 39, 40). Among the references indicated, Siebenrock (1902), Williams (1954a), Pritchard and Trebbau (1984), do provide descriptive information particularly useful in preserved specimens but few comparative osteologic characters.

### *Podocnemis erythrocephala* (Spix, 1824)

SYNONYMY: Authors before 1974 used *P. cayennensis* (Schweigger, 1812) for this species. See Wermuth and Mertens (1961, 1977),

Mittermeier and Wilson (1974), Pritchard and Trebbau (1984), Iverson (1992), Bickham et al. (2007; however, usage of *cayennensis* was not "brief," ibid.: 187) for further discussion and references.

TYPE SPECIMEN AND LOCALITY: See Mittermeier and Wilson (1974), Iverson (1992).

DIAGNOSIS: See Siebenrock (1902), Mittermeier and Wilson (1974), Pritchard and Trebbau (1984).

REFERRED MATERIAL: USNM 135474, AMNH 111069, DGM 45RR.

PREVIOUS WORK: Earlier authors (e.g., Boulenger, 1889; Siebenrock, 1902; Williams, 1954a) did not recognize this species, which is involved in the "*cayennensis*" type question discussed in Mittermeier and Wilson (1974), see also Pritchard and Trebbau (1984) and Iverson (1992). Mittermeier and Wilson (1974) figure and describe skull and shell. Groombridge (1982) has general references.

### *Podocnemis bassleri* Williams, 1956

TYPE SPECIMEN: AMNH 1662, a nearly complete skull figured by Williams (1956: figs. 1, 3–5).

TYPE LOCALITY: Rio Aguaytia, eastern Peru, about 8°10′S, 75°15′W fide Williams (1956).

HORIZON: Tertiary, probably Late Miocene, Contamana Group fide Williams (1956). See Gaffney et al. (1998) and Meylan et al. (2009) for further comments and references for Contamana Group chronology.

DIAGNOSIS: "Close to *Podocnemis expansa*, differing only in the apparently larger size, in the relationship of the internal palatal processes of the maxillae (which project abruptly dorsally and do not lie extended anteroposteriorly as in the Recent species), and in the slightly shorter relative distance from snout tip to posterior borders of the orbits" (Williams, 1956: 2).

PREVIOUS WORK: Only Williams (1956) has dealt with this species. Wood and Diaz de Gamero (1971) state that this species is either ancestral to or closely related to *Podocnemis expansa*.

DISCUSSION: The nearly indistinguishable skulls of *P. bassleri* and *P. expansa* suggest that the age of the fossil was Williams' main criterion for differentiating the taxa. It could be synonymized with *P. expansa*. In any case, this skull is the oldest definite record for the *Podocnemis* clade, here termed the magnatribe Podocnemidand, as *"P." negrii* (Carvalho et al., 2002) does not preserve any of the diagnostic characters of the genus *Podocnemis* and is placed as Podocnemididae incertae sedis (see below), and the specimen of *Cerrajonemys* is too poorly preserved to be sure of its diagnostic characters, also Podocnemididae incertae sedis (see below).

## Magnatribe Erymnochelydand Broin, 1988, new rank

DIAGNOSIS: Members of infrafamily Podocnemidodda; cheek emargination slight to absent in contrast to *Podocnemis* (reversed in *Cordichelys* and *Bairdemys*); fossa precolumellaris shallow to absent, not deep (except in *Erymnochelys*).

INCLUDED TAXA: *Peltocephalus* Duméril and Bibron, 1835; *Erymnochelys* Baur, 1888; *Bairdemys* Gaffney and Wood, 2002; *Dacquemys* Williams, 1954c; *Neochelys* Bergounioux, 1954; *Shweboemys* Swinton, 1939; *Bauruemys* Kischlat, 1994; *Stereogenys* Andrews, 1901; *Caninemys* Meylan, Gaffney, and Campos, 2009; *Turkanemys* Wood, 2003; *Neochelys* Bergounioux, 1954; *Papoulemys,* Tong, 1998; *Mogharemys,* n. gen.; *Cordichelys,* n. gen.; *Latentemys,* n. gen.; *Brontochelys,* n. gen.; *Albertwoodemys,* n. gen.; *Lemurchelys,* n. gen.

DISCUSSION: Rather than completely reflect the cladogram within this group (see fig. 98) in the classification with new categories and taxa, we only list the paraphyletic taxa outside the tribe Stereogenyini.

### *Caninemys* Meylan, Gaffney, and Campos, 2009

TYPE SPECIES: *Caninemys tridentata* Meylan, Gaffney, and Campos, 2009.

INCLUDED SPECIES: *Caninemys tridentata.*

DISTRIBUTION: Late Tertiary, Miocene, of Acre, Brazil.

ETYMOLOGY: Named for the bulldog appearance of the skull and the large maxillary processes in the position of mammalian canines.

TABLE 3
**Species of the Tribe Stereogenyini**

| | *Mogharemys blanckenhorni* | *Bairdemys venezuelensis* | *Bairdemys hartsteini* | *Bairdemys sanchezi* | *Bairdemys winklerae* | *Latentemys plowdeni* | *Cordichelys antiqua* | *Brontochelys gaffneyi* | *Shweboemys pilgrimi* | *Stereogenys cromeri* | *Lemurchelys* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Distribution | Egypt | Venezuela | Puerto Rico | Venezuela | Venezuela | Egypt | Egypt | Pakistan | Burma | Egypt | Egypt |
| Prefrontal-frontal strongly convex dorsally in lateral view | no | yes | yes | yes | no | no | no | no | no | no | no |
| Degree of temporal emargination | ? | less | less | more | less | ? | less | ? | ? | less | ? |
| Amount of jugal entering orbital rim | large | large | large | large | ? | large | small | large | large | large | large |
| Ventral margin of orbit a sharp edge | yes | yes | yes | yes | yes | yes | yes | no | yes | yes | no |
| Frontal exposure in orbital rim | ? | intermediate | intermediate | intermediate | ? | intermediate | large | large | intermediate | intermediate | small |
| Parietal-palatine contact | no | no | no | no | ? | no | no | no | yes | yes | no |
| Antrum postoticum | small, tubular | very small, flat | very small, flat | very small, flat | ? | small, tubular | small tubular | ? | ? | | small, tubular |
| Labial ridge | low and thick | deep and narrow | deep and narrow | deep and narrow | deep and narrow | deep and narrow | deep and narrow | low and thick | low and thick | low and thick | low and thick |
| Triturating surface convexity | absent | deep | deep | shallow | ? | shallow | shallow | shallow | shallow | shallow | shallow |
| Pinched snout | ? | no | no | no | no | no | yes | ? | yes | no | yes |
| Elongated snout | no | no | no | no | yes | no | no | no | no | no | no |
| Angle of front of skull | 80° | 90° | 90° | 70° | 50° | 65° | 80° | 95° | 100° | 95° | 105° |
| Triturating surface with 2 pairs of accessory ridges | yes | no | no | no | no | no | no | no | no | no | no |
| Accessory ridge on premaxilla | ? | no | no | no | no | ? | no | ? | no | yes | no |
| Extent of secondary palate | absent | less | less | less | less | less | less | less | more | more | less |
| Pterygoids meeting in midline | yes | yes | yes | yes | ? | yes | no | yes | no | no | yes |
| Eustachian tube exit separated by bone from stapedial artery entrance in fenestra postotica | no | yes | yes | yes | ? | yes | no | ? | ? | probably no | no |

TABLE 3
*(Continued)*

| | *Mogharemys blanckenhorni* | *Bairdemys venezuelensis* | *Bairdemys hartsteini* | *Bairdemys sanchezi* | *Bairdemys winklerae* | *Latentemys plowdeni* | *Cordichelys antiqua* | *Brontochelys gaffneyi* | *Shweboemys pilgrimi* | *Stereogenys cromeri* | *Lemurchelys* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Ventral vertical flange on squamosal | no | yes | yes | yes | yes | no | no | ? | no | ? | ? |
| Deep supraoccipital base | no | no | no | no | no | no | no | ? | no | no | yes |

DIAGNOSIS: A podocnemidid pleurodire with a well-developed processus trochlearis pterygoidei, quadrate-basioccipital contact, and a large cavum pterygoidei; unique among podocnemidids (and all other turtles) in having greatly inflated maxillae, each with a ventral, toothlike process that, together with a single process formed on the midline of the premaxillae, form a tridentate condition in the upper triturating surfaces, unique among pleurodires. The entire animal was probably smaller than *Stupendemys geographicus* Wood.

### *Caninemys tridentata* Meylan, Gaffney, and Campos, 2009

TYPE SPECIMEN: MCT 1496-R, a nearly complete skull collected by L.I. Price in 1962.

TYPE LOCALITY: Locality 28 of L.I. Price, Volta de Pedra Pintada, upper Rio Jurua, Acre, Brazil.

HORIZON: Late Miocene (Meylan et al., 2009).

DIAGNOSIS: Same as for the genus.

ETYMOLOGY: The species epithet is based on the tridentate appearance of the skull that is most clearly seen in anterior view.

PREVIOUS WORK: Meylan et al., 2009.

DISCUSSION: Although this taxon cannot be differentiated from the shell-based *Stupendemys geographicus* Wood, 1976, because there is no overlap in presently known morphology, it is likely that *Caninemys* is significantly smaller than the Venezuelan *Stupendemys*. Using skull-shell ratios of recent specimens of *Podocnemis expansa* and other recent podocnemidid species, it is hypothesized that the shell of *Caninemys* would be less than 4–5 ft in length rather than the 7+ ft length of *Stupendemys*. For comparison, the largest skulls of recent *Podocnemis expansa* have a condylobasal length of about 12 cm (Williams, 1956) and the Mio-Pliocene *Podocnemis bassleri* (Williams, 1956; very similar to *P. expansa* in morphology) is 15.7 cm in length, compared to about 16.5–17.0 cm for *Caninemys*. It is possible that smaller species of *Stupendemys* were present in the Acre region and that *Caninemys* is the skull of one of these, but that is only speculation (Meylan et al., 2009).

*Dacquemys* Williams, 1954b

TYPE SPECIES: *Dacquemys paleomorpha* Williams, 1954b.

INCLUDED SPECIES: *Dacquemys paleomorpha.*

DISTRIBUTION: Late Eocene to early oligocene of Egypt.

DIAGNOSIS: A genus of podocnemidid pleurodire known only from the skull; characterized by the unique possession of a fully roofed temporal region with a posteriorly extensive parietal and wide supraoccipital completely covering the otic chamber in dorsal view; broad parietal-squamosal contact not seen in other podocnemidids, except the unnamed UCMP 42008; prefrontal extends to anterior margin of apertura narium externa as in *Peltocephalus* but in contrast to *Podocnemis*, interorbital distance very wide with orbits facing laterally in contrast to living Podocnemididae; maxillae meet broadly behind premaxillae; premaxillae recessed and not visible laterally in contrast to all other Pelomedusoides; vomer absent; anterior part of triturating surface more extensive than in living Podocnemididae but secondary palate as seen in *Shweboemys* group absent; two accessory maxillary ridges meet anteriorly to form enclosed trough unique to this genus; antrum postoticum small as in *Podocnemis*; precolumellar fossa shallow as in *Podocnemis expansa*; pterygoid-jugal contact absent.

*Dacquemys paleomorpha* Williams, 1954b

TYPE SPECIMEN: SMNS 12645, a nearly complete skull without lower jaws, lacking parts of the left side and the central basicranial region (Dacqué, 1912: pl. 2, figs. 6–8; Gaffney, 1979: fig. 128; Williams, 1954b: pl. 1; Gaffney et al., 2002: figs. 2 and 3).

TYPE LOCALITY AND HORIZON: Dacqué (1912) gave the locality at first in reference to a shell: "Unteroligocäne Fluviomarinestuffe nördlich der Birket Qerun; nordlich non Tamieh; ostlich vom Schweinforthplateau. Schädel: aus derselben stufe bei Dimêh. Alles Fayum" (ibid., p. 310). Williams (1954b, repeated in Gaffney, 1979) has the locality as "Diieh" which seems to be a misspelling of "Dimêh." The reference to the skull "from the same sediment near Dimêh" presumably means the Qasr el-Sagha or Birket Qarun Formations of late Eocene age.

REFERRED MATERIAL: DPC 5986 (Gaffney et al., 2002: figs. 4, 5), partial skull lacking anterior part of palate and some of left side. Field No. 86-292, collected by Alex van Nievelt. B-4 (lower Jebel Qatrani Fm., 1/4 mile southeast of A), AMNH quarry B area, early Oligocene (Seiffert, 2006).

Possibly BMNH R3346, a lower jaw figured by Williams (1954b; previously identified by Andrews, 1906, as *Podocnemis fajumensis*) that fits the triturating surface of the maxilla in *Dacquemys*, as argued by Williams.

PREVIOUS WORK: Williams (1954b). Gaffney et al. (2002) provides a redescription based on two specimens and a reconstruction of the skull.

DISCUSSION: There is no support for the earlier suggestions that the shell for *Dacquemys paleomorpha* is the shell-based species, *Podocnemis fajumensis* Andrews, 1903 (Williams, 1954b; Lapparent Broin, 2000a). We argue below that *fajumensis* is the shell of a *Neochelys* species. We have concluded that based on skull morphology, *Dacquemys* is the sister taxon to UCMP 42008, which has a very unusual shell similar to that of *Albertwoodemys.* The possibility exists that *Dacquemys* is the skull for *Albertwoodemys,* as both are known from the early Oligocene of the Fayum.

***Albertwoodemys,*** new genus

*Albertemys* nomina nuda Auffenberg, 1981.

TYPE SPECIES: *Albertwoodemys testudinum,* new species.

DISTRIBUTION: Oligocene of Egypt.

ETYMOLOGY: For Albert E. Wood, father of one of the authors, Roger C. Wood, and a founding member of the Society of Vertebrate Paleontology, as well as a past president, honorary member, and recipient of the Romer-Simpson medal of that society.

DIAGNOSIS: A podocnemidid pleurodire known only from the shell with these unique features: single pair of scales on plastron between gular scales and abdominal scales (could be interpreted as absence of pectoral or humeral scale or fusion of the two); very small anal scales not meeting in midline

accompanied by deep, C-shaped anal notch; scale sulci lying on raised ridges rather than incised on bone surface; large raised, swellings on lateral edges of posterior plastral lobe; entire shell more highly domed than any other podocnemidid; other distinguishing features: arcuate ischial contacts, with convex sides facing midline; ridge on visceral surface of posterior peripherals; large intergular scale separating small gular scales that do not reach entoplastron.

DISCUSSION: The specimen here named *Albertwoodemys testudinum* was described and named in an unpublished Ph.D. dissertation by R. Wood in 1971. Wood coined the name *"Albertemys"* for this specimen, but the dissertation and the name were never published by Wood. Auffenberg (1981), in his description of Olduvai fossil turtles, had access to Wood's dissertation and compared his new taxon, *Latisternon,* to a number of pleurodires, including "*Albertemys* Wood, 1970" (1981: 512, although the dissertation date is actually 1971). It is apparent in the bibliography of Auffenberg (1981: 522) "Unpubl. PhD Diss...." that the author was aware of the fact that the dissertation was not an actual publication. A species name is not mentioned but there are characters for *"Albertemys"* indicated in the comparison with *Latisternon.* As it lacks a type species and type specimen, the name *"Albertemys"* is a nomen nudum.

***Albertwoodemys testudinum,*** n. gen. et sp.

TYPE SPECIMEN: AMNH 5088 (figs. 83, 84), plastron with articulated left lateral and posterior peripherals.

TYPE LOCALITY: One mile west of AMNH quarries in the Lower Fossil Wood zone (Simons, 1968: 21), Fayum Depression, Egypt.

HORIZON: Jebel Qatrani Fm., early Oligocene (Seiffert, 2006).

DIAGNOSIS: As for genus.

ETYMOLOGY: In reference to the high-domed, tortoiselike nature of the shell.

REFERRED MATERIAL: None, but a shell, KNM-WK17139, from the Miocene of Kalodirr, Kenya, is very similar and may be the same species or genus.

PREVIOUS WORK: Described in Wood (1971).

DISCUSSION: It may seem the epitome of self-indulgent hypocrisy to name another new shell taxon, particularly after thoroughly criticizing those who have done so (Gaffney et al., 2006). However, we have a good reason (doesn't everyone?) for breaking our own rules. *Albertwoodemys testudinum* is both diagnosable and subject to phylogenetic analysis, just not right now. The key to the relationships of *Albertwoodemys* lies in the skull of UCMP 42008 (currently under study by Bramble, Hutchison, and Gaffney), which has a shell with a number of synapomorphies in common with *Albertwoodemys.* The skull, however, is not yet named and described, although we have enough information to place it in the cladogram as the sister taxon to *Dacquemys* (fig. 98). *Albertwoodemys* is probably the sister taxon to UCMP 42008 or it could be the shell of *Dacquemys* itself (although *Dacquemys* is Eocene, it is very late Eocene and *Albertwoodemys* is very early Oligocene), in any case, it is clearly closely related to UCMP 42008 and *Dacquemys.* So we name the plastron with the presumption that description of the skull of UCMP 42008 will clarify its relationships.

DESCRIPTION: There are several unique features on the plastron (figs. 83, 84). The humeral and pectoral scales are either fused or one or the other of these pairs of scales is totally missing. The anal scales are so small and posteriorly placed that they make no contact at all along the midline. On the inner surface of the posterior lobe of the plastron parallel to and just inside the lateral borders are bulbous ridges of unknown significance. All of these features are unique in pleurodires.

Excellent preservation characterizes the only known specimen of *Albertwoodemys.* The anterior lobe of the plastron is relatively short and rounded; the posterior lobe is somewhere between 1.5 and 2 × as long as the anterior one. The bridge is unusually long, being nearly twice as long as the posterior lobe. The lateral borders of the posterior lobe converge only slightly toward the midline as they extend posteriorly. The tips of the xiphiplastra are sharply pointed and separated from each other by a deeply incised U-shaped notch. Based on UCMP 42008 and specimens associated with it, a caudal buckler or osteoderm apparently fits

here. The ventral surface of the plastron is a convex bulge curving gently from anterior to posterior. On either side of the midline in the area of the hypo-xiphiplastral sutures are localized oval depressions reversing this trend. A slight transverse concavity is present between the bridges at right angles from the midline. The plastron measures 43.1 cm in length.

In anteroposterior cross section (fig. 84B, C) the epiplastra are wedge shaped, so that the greatest thickness occurs posteriorly at the junction between the epiplastra and the entoplastron. This thickening, however, is not uniform, and the resultant structure is not truly comparable to the epiplastral thickening and excavation present in nearly all Testudinidae. Instead, between the laterally situated ridges there is a concavity on the midline suture anteriorly (figs. 83, 84). The entoplastron affords a striking example of how the shape of a bone may vary between the exterior and interior of a chelonian shell. Ventrally it is roughly diamond shaped, while dorsally it is a trapezoid whose leading edges are so shallow that its shape might almost be described as that of an equilateral triangle (fig. 83B).

Superimposed on the dorsal surface of the entoplastron is a Y-shaped ridge whose open end faces anteriorly. The distal ends of the bifurcated arms lead into the transverse ridges just described at the posterior edges of the epiplastra. Along the lateral border of the inner surface of the posterior lobe of the plastron are paired bony protuberances. These structures extend over an area covering the posterior portion of the hypoplastron and an adjacent region on the anterior end of the xiphiplastron (fig. 84D).

Prominent pelvic scars are also present on the inner surface of the plastron. The posterolateral ends of the ischial scars are continuous with the U-shaped anal notch and then curve forward until the proximal ends are nearly parallel to each other and the midline. This entire paired structure is slightly raised on a pedestal above the inner plastral surface. The pubic scars are spaced in the form of obtuse-angled triangles whose apices are directed posterolaterally. A very small portion of the right pubis has been preserved, which shows that the basal thickness quickly diminishes to produce a blade-like leading edge. Noting else is known of the pelvis.

The bone sutures on the plastron of *Albertwoodemys* are consistent with a typical podocnemidid. Roughly trapezoidal epiplastra form the anteriormost portion of the plastron. Immediately behind these paired elements is the more or less diamond-shaped entoplastron, whose posterior extension lies behind the level of the axillary notches of the bridge. This same condition can be seen in *Neochelys*. Sutures between the hyoplastra and hypoplastra bisect the middle of the bridge and terminate laterally in a junction with the mesoplastral sutures. The mesoplastra themselves are roughly hexagonal elements. Sutures separating the hypoplastra from the xiphiplastra diverge laterally and posteriorly from the midline at an angle of approximately 75°.

Scale sulci on the plastron of *Albertwoodemys* are very clearly incised. Consequently, the absence of a humero-pectoral sulcus cannot be attributed to inadequate preservation. Much as in most living and extinct Testudinidae, the scale furrows are not simply grooves on the bony surface of the plastron, but are instead enclosed within slightly raised parallel ridges. At the front of the plastron, the pentagonal intergular scale is extremely large and broad. Small triangular gulars are wedged in on either side of the anterior end of the intergular. The pectoral-abdominal sulcus traverses the belly of the plastron anterior to the mesoplastra. The position of the abdominal-femoral sulcus is in no way remarkable. But at the posterior end of the plastron, the anal scales are so reduced that they are prevented from meeting at the midline by the xiphiplastral notch.

At both the anterior and posterior ends of the plastron, the scales extended far onto the dorsal surface of the plastron (fig. 83B). Anteriorly, most of the visceral surface of the epiplastra was covered by scales. The trapezoidal prolongation of the intergular was flanked on either side by rhombic gulars. In contrast to the situation for these scales on the external surface of the plastron, the combined areal extent of the two gulars exceeded that of the intergular. Triangular wedges of the pectoral scales stretched from

the lateral borders of the gular scales back to the axillary notch. On the posterior lobe of the plastron, the femoral scales extend dorsally to cover the outer surface of the lateral bony ridges. Apparently the anal scales completely encompassed the tips of the xiphiplastra, encircling them in glovelike fashion.

Part or all of six peripheral bones have been preserved on the left side. Assuming that *Albertwoodemys* had the usual chelonian complement of 11 peripherals, it is probable that numbers five through 10 are represented. A lateral carina is lacking, and the vertical orientation of the peripherals shows that the carapace was high vaulted and rounded (as in UCMP 42008 and the Kalodirr shell) rather than being low and flat as in typical aquatic forms. Unlike any tortoise, however, the distal ends of the pleural scales extend well down onto the peripheral bones in agreement with the pattern encountered in pleurodires, emydids, and baenids. The sulcus separating what is probably the sixth marginal scale from the abdominal scale crosses the distal portion of the mesoplastron in a manner similar to that seen in the type of "*Stereogenys*" *libyca* (Andrews, 1906: 303, fig. 97). An unusual feature on the inner surface of the posterior peripherals is a thick ridge (fig. 84E), which continues forward and around the circumference of the inguinal notch as a bladelike crest that ultimately connects to the anterior extension of the thick ridge on the inner surface of the posterior lobe of the plastron. Such a structure is often found in testudinids but never in pleurodires.

The depositional environment of the Jebel Qatrani Fm. has been described as "fluviomarine," but Simons (1968: 15, 16) and Bown and Kraus (1988) indicate a more terrestrial depositional environment, with channel sands and conglomerates together with clayey flood plains deposits reinforcing this interpretation. The tortoiselike structure of the shell of *Albertwoodemys*, suggests that it (and UCMP 42008) was a terrestrial form.

### UCMP 42008, unnamed new genus and species

DIAGNOSIS: Podocnemidid known from skull and shell; differing from all other pleurodires on the basis of these characters: triangular-shaped and fully roofed skull, cheek and temporal emargination completely absent, due to unique possession of unusually large squamosal with ventral flange on occipital surface and extensive parietal contact, laterally and anteriorly expanded supraoccipital with extensive squamosal and parietal contacts (longer than in *Dacquemys*, the only form to approach it), large quadratojugal with extensive squamosal and jugal contacts; anteriorly extensive prefrontal with very long maxilla contact and ventral flange forming snout region; apertura narium externa small and partially subdivided on midline; other distinguishing characters: orbits facing anterolaterally; interorbital groove absent; medial expansion of triturating surface present, median maxillary ridge present, accessory ridge present; complete cavum pterygoidei present; processus trochlearis pterygoidei present and at right angles to midline; carapace high domed with deep nuchal embayment; caudal buckler or cloacal cover formed by fused osteoderms.

SPECIMEN: UCMP 42008, skull lacking major portions of palate and braincase, partial shell with carapace and plastron elements.

LOCALITY: UCMP locality V4898, Moruorot Hill (often alternately spelled Muruarot Hill), 20 miles NE of Lodwar, north-central Kenya.

HORIZON: Early Miocene Lothidok Formation (Boschetto et al., 1992).

REFERRED MATERIAL: A caudal buckler, UCMP 41918, and a peripheral, UCMP 42141, both from UCMP locality V48100, are identified with this taxon. It should be mentioned that National Museum of Kenya WK-17139, a shell from the Miocene of Kalodirr, Kenya, is very similar to the shell of UCMP 42008 and may be the same species or genus.

DISCUSSION: UCMP 42008 is currently being studied by J.H. Hutchison, D. Bramble, and E.S. Gaffney. Enough work has been done to include it in the phylogenetic analysis. The unusual shell morphology of this specimen links it with *Albertwoodemys,* based on the high-domed carapace, the deeply incised anterior margin of carapace, thickened plastral edges, and the fusion (or loss) of the

humeral and pectoral scales. See discussions under *Dacquemys* and *Albertwoodemys.*

*Turkanemys* Wood, 2003

TYPE SPECIES: *Turkanemys pattersoni* Wood, 2003.

INCLUDED SPECIES: *Turkanemys pattersoni* Wood, 2003.

DISTRIBUTION: Late Miocene Nawata Formation, early Pliocene Kanapoi Formation, and Mio-Pliocene sediments west of Ekora, northwestern Kenya (Wood, 2003).

DIAGNOSIS: A podocnemidid known from the skull and postcrania; skull relatively high and narrow in contrast to *Bauruemys*; orbits facing laterally in contrast to *Podocnemis*; interorbital groove such as found in *Podocnemis* absent; temporal emargination less than in *Podocnemis*; parietal-quadratojugal contact long; cheek emargination present but not reaching to dorsal edge of orbit; postorbital large in contrast to *Podocnemis*; medial expansion of triturating surface, median maxillary ridge, present; two accessory ridges present on triturating surface in contrast to *Erymnochelys* and *Peltocephalus,* ridges deep in contrast to all other Erymnochydand; vomer absent; fossa precolumellaris present and shallow as in *Peltocephalus* but in contrast to *Erymnochelys*; foramen jugulare posterius closed; jugal-quadrate contact absent in contrast to *Erymnochelys* and *Peltocephalus*; horizontal occipital present in contrast to *Erymnochelys* and *Peltocephalus*; chorda tympani enclosed in processus retroarticularis.

Postcrania with cervical centra saddle shaped but not identical to those in *Peltocephalus*; nuchal bone width greater than length; six neurals extending to costal six; first neural four sided; pectoral scales do not contact mesoplastra, but do contact entoplastron and epiplastra.

DISCUSSION: *Turkanemys* provides another glimpse of the podocnemidid record in the African Miocene providing further evidence that there is much to be learned about the relationships of *Erymnochelys* and *Peltocephalus* from the fossil record. The shell of *Turkanemys* is very similar to that of *Erymnochelys,* particularly in the classically influential area of the anterior plastral lobe, in that it has medially meeting gular scales rather than separated ones as in *Peltocephalus.* In our resolution, the MPC shows *Turkanemys* as the sister taxon to (*Erymnochelys, Peltocephalus*) + remaining magnatribe Erymnochelydand. A close alternative would be *Turkanemys* as the sister taxon to (*Erymnochelys, Peltocephalus*). Unfortunately some potentially decisive characters in *Turkanemys* are missing due to lack of preparation, in particular the condition of the anterior opening of the cavum ptergoidei. So future work may resolve these relationships. Nonetheless, *Turkanemys* is clearly a member of the magnatribe Erymnochelydand, with close similarities to both *Erymnochelys* and *Peltocephalus.*

Cervical vertebrae 4–7 of both *Erymnochelys* and *Turkanemys* are very similar to each other in being wider than high and differ from other Podocnemidinae (as defined here) in lacking the well-developed heterocoely or saddle-shaped centra. This condition could be interpreted as an intermediate between the *Podocnemis* fully heterocoelous centra that wrap around posterolaterally and the condition seen in the basal podocnemidid, *Bauruemys.* Nonetheless, our analysis still places *Turkanemys* outside *Erymnochelys* + *Peltocephalus* requiring the wide articular condition to be acquired twice, despite the proximity of these taxa in the cladogram. Again, this is only a few steps away from a group containing *Erymnochelys, Peltocephalus,* and *Turkanemys.* We feel that although our MPC resolves these three taxa, in view of the missing data for *Turkanemys* it would be more realistic to conclude that the three are an unresolved trichotomy at present.

Another as yet incompletely described piece of the *Erymnochelys-Peltocephalus* puzzle may be a specimen from Kenya. Witmer (1990) published an abstract announcing a new fossil from the lower Miocene of Rusinga Island, Kenya. This well-preserved specimen, KNM-RU 18401, consists of an articulated skull, shell, cervicals, and appendicular elements, and has been examined by us in the KNM. This as yet unnamed specimen has what appears to be a quadratejugal contact that partially closes the check emargination, similar to that seen in *Erymnochelys* and *Peltocephalus.* It has a shallow

fossa precolumellaris and a posterior cervical that is almost identical with one from *Turkanemys*. The Rusinga skull has a surface coating of matrix obscuring sutures, which needs to be removed before the very tentative sutures reported here can be accepted. Because of this and the fact that the lower jaws are still attached to the skull by matrix, we feel that there are insufficient characters to use this specimen in our character matrix. Although Witmer mentions the presence of an interorbital groove characteristic of *Podocnemis*, our own examination suggests that the widely spaced orbits of the Rusinga skull have a shallow midline depression not homolgous to the distinctly formed, interorbital groove seen between the very closely spaced orbits of *Podocnemis*. Nonetheless, we agree completely with Witmer's conclusions (1990: 49A): "the Rusinga turtle is a member of a clade that was relatively diverse on mainland Africa, but that today exhibits a relict distribution."

*Turkanemys pattersoni* Wood, 2003

SYNONYMY: None.

TYPE SPECIMEN: KNM-LT 569, a shell, skull, and associated axial and partial appendicular skeleton (see Wood, 2003: 117, 118) for more detailed description of type.

TYPE LOCALITY: Lothagam, Kenya (Wood, 2003).

HORIZON: Lower member of the late Miocene Nawata Formation (Wood, 2003; see also other articles in same volume).

REFERRED MATERIAL: Specimens listed in Wood (2003). See also discussion below under *Erymnochelys*.

PREVIOUS WORK: See Wood (2003) for figures and description of skull and shell.

*Erymnochelys* Baur, 1888

TYPE SPECIES: *Dumerilia madagascariensis* Grandidier (1867).

INCLUDED SPECIES: *Erymnochelys madagascariensis*.

DISTRIBUTION: Recent of Madagascar, possibly Miocene-Pliocene of eastern Africa. There have been a number of records of shell material identified as *Erymnochelys* sp. or as something similar to *Erymnochelys* (see Lapparent de Broin, 2000a, for summary and literature). Most of these are relatively fragmentary and, as far as can be determined from the publications, lack generic level diagnostic characters. However, Hirayama (1992) described shells and a posterior cervical from the Mio-Pliocene Sinda beds of the Democratic Republic of Congo (formerly Zaire) that are better preserved. The shells have a small intergular with medially meeting gular scales, diagnostic of *Erymnochelys* among the Recent fauna. The cervical is nearly identical to one of the cervicals in *Erymnochelys,* in that it is wider than high and lacks the saddle-shaped centra. However, considering the more recent additions to the fossil record, particularly *Turkanemys* and possibly related taxa, it is less likely that the Sinda material can be reliably identified as *Erymnochelys*. Among the published records, it is clear that the magnatribe Erymnochelydand has a long record in Africa that is only now being documented. The relatively conservative shell morphology in this group must be kept in mind when identifying shell material.

There is, however, undescribed skull material that can possibly be identified as *Erymnochelys*. Partial skulls and shell material in the MAC identified by label as coming from Miocene beds in the Sinda/Mohari region, western rift valley, Democratic Republic of Congo, consist of MAC RG1368A, MAC RG2626, MAC RG13686B, and MAC uncataloged. All are anterior portions of the skull, and all unfortunately lack any part of the cheek or basicranium. Although the preserved areas agree closely with the Recent *Erymnochelys*, the diagnostic characters of the cheek and basicranium are missing, making it possible that these specimens represent a taxon different from *Erymnochelys*.

DIAGNOSIS: A podocnemidid known from the skull and postcrania; skull relatively high and narrow in contrast to *Bauruemys*; orbits facing laterally in contrast to *Podocnemis*; interorbital groove such as found in *Podocnemis* absent; temporal emargination less than in *Podocnemis*; parietal-quadratojugal contact long; cheek emargination absent; postorbital large in contrast to *Podocnemis*; medial expansion of triturating surface, median maxillary ridge, present; accessory ridge or ridges present in triturating surface;

vomer absent; fossa precolumellaris deep and well defined as in *Podocnemis unifilis*; foramen jugulare posterius closed; jugal-quadrate contact present in contrast to all other podocnemidids except *Peltocephalus* and UCMP 42008; cavum pterygoidei with large anterior opening and foramen cavernosum in roof; horizontal occipital shelf absent; chorda tympani enclosed in processus retroarticularis.

Postcrania with cervical centra not saddle shaped but not the same as in *Bauruemys*; nuchal bone width greater than length; six neurals extending to costal six; first neural four sided; axillary buttress reaches peripheral two in contrast to *Peltocephalus*; axillary musk duct in buttress not in bridge; pectoral scales do not contact mesoplastra, but do contact entoplastron and epiplastra; gular scales meet on midline.

DISCUSSION: Use of *Erymnochelys* and *Peltocephalus* goes back to Dumeril and Bibron (1835) and Baur (1888), but it was the synonymization with *Podocnemis* by the influential Boulenger (1889) catalog that curtailed their use, despite Baur's (1890) argument against synonymy, until Williams (1954c) began their more recent resurrection. In that paper Williams, agreeing with Baur (1890), Siebenrock (1902), and Müller (1935), proposed that *Peltocephalus* was allied with the African forms and not with the other South American ones, differing from the hypotheses of Dacqué (1912) and Zangerl (1948). Later, more widespread use of the three genera by Frair et al. (1978), Gaffney (1979), and others normalized the revival of the three genera.

Baur (1890: 483) published the following comparative diagnoses of the osteology of the three Recent podocnemidid genera in opposition to Boulenger's sinking of them into *Podocnemis*:

> "*Podocnemis,* Wagler
> Jugal and quadrate bones separated; articular faces of anterior cervicals saddle shaped; first intercentrum small and free. Type: *P. expansa*, Schweigg.
>
> "*Peltocephalus*, Dum. and Bib.
> Jugal and quadrate in contact. articular faces of anterior cervical saddle shaped; first intercentrum large and suturally united with neuroids and centrum of atlas. Interparietal shield triangular with base behind. Type: *P. tracaxa*, Spix.
>
> "*Erymnochelys*, Baur
> Jugal and quadrate in contact; articular faces of cervicals not saddle shaped; first intercentrum large and suturally united with neuroids and centrum of atlas. Interparietal shield triangular with base in front. Tpye [sic]: *E. madagascariensis*, Grand."

Despite examining specimens, we have been unable to substantiate the atlas character in *Podocnemis*. The other characters became very influential systematically and appear in nearly all phylogenetic treatments of the Podocnemididae over the past 120 years, including the present one.

### *Erymnochelys madagascariensis* (Grandidier, 1867)

SYNONYMY: See Boulenger (1889), Baur (1890), Tronc and Vuillemin (1974), Wermuth and Mertens (1977).

TYPE SPECIMEN: MNHN Herpetology 9544 (Iverson, 1992).

TYPE LOCALITY: West coast of Madagascar (Iverson, 1992).

REFERRED MATERIAL: Specimens that we used are as follows: AMNH Herpetology 63579, AMNH Herpetology 63574, MCZ 5198, MNHN Herpetology 92.494 DD67, NMV 1813, NMV 139, NMV 138, NMV 1839, NMV 1840, NMV 1811, NMV 1810, NMV 1475, NMV 1476, NMV 843/20, NMV 2518/0, NMV 847/1920, YPM 15398.

Possible subfossil specimens from Madagascar: DPC 11870, skull and jaws, "Anjohibe near Q' exit, 92-M-327" (label); DPC 3797, skull and jaws, "Anjohibe, 83-310" (label).

PREVIOUS WORK: See Discussion above. Literature on this species can be found in Iverson (1992). Also see Wermuth and Mertens (1961, 1977) for synonymies and further references; Kuchling (1993) has ecologic and other information and references. Williams (1954a) figures the palate. The paper by Tronc and Vuillemin (1974) is difficult to find, but has a useful review of the literature on *Erymnochelys madagascariensis* and de-

scription of its osteology with the most figures of any Recent podocnemidid.

*Peltocephalus* Dumeril and Bibron, 1835

TYPE SPECIES: *Emys tracaxa* Spix (1824) = *Emys dumeriliana* Schweigger (1812), by monotypy fide Iverson (1992).

INCLUDED SPECIES: *Peltocephalus dumerilianus.*

DISTRIBUTION: Northern South America.

DIAGNOSIS: A podocnemidid known from the skull and postcrania; skull relatively high and narrow in contrast to *Bauruemys*; elongate, pinched snout in contrast to all podocnemidids except tribe Stereogenyini; orbits facing laterally in contrast to *Podocnemis*; interorbital groove such as found in *Podocnemis* absent; temporal emargination less than in *Podocnemis*; parietal-quadratojugal contact long; cheek emargination absent; postorbital large in contrast to *Podocnemis*; medial expansion of triturating surface, median maxillary ridge, present; accessory ridge or ridges present in triturating surface; vomer absent; fossa precolumellaris shallow as in *Podocnemis expansa* and in contrast to deep as in *Erymnochelys*; foramen jugulare posterius closed; jugal-quadrate contact present in contrast to all other podocnemidids except *Erymnochelys* and UCMP 42008; cavum pterygoidei with large anterior opening and foramen cavernosum in roof; horizontal occipital shelf absent; chorda tympani enclosed in processus retroarticularis.

Postcrania with cervical centra saddle shaped; nuchal bone width greater than length; six neurals extending to costal six; first neural four sided; axillary buttress reaches peripheral three in contrast to *Erymnochelys*; axillary musk duct in buttress not in bridge; pectoral scales do not contact mesoplastra, but do contact entoplastron and epiplastra.

DISCUSSION: Previous literature on this species can be found in Iverson (1992). See *Erymnochelys* discussion for original Baur (1890) diagnoses of Recent genera.

*Peltocephalus dumerilianus* Schweigger, 1812

SYNONYMY: See Boulenger (1889, as *P. tracaxa*), Iverson (1992).

TYPE SPECIMEN: Apparently lost (Iverson, 1992).

TYPE LOCALITY: "America meridionali" (Iverson, 1992).

REFERRED MATERIAL: Specimens that we have seen are: NFWFL 337, NFWFL 336, AMNH Herpetology 131886, MCZ 93077, DGM 361-RR, USNM Herpetology 44760 (= 257687), USNM Herpetology 44761 (= 257688), FMNH Herpetology 140281.

PREVIOUS WORK: See Siebenrock (1902, as "*Podocnemis dumeriliana*"), Wermuth and Mertens (1961, 1977) for synonymies and further references, also Pritchard and Trebbau (1984). Williams (1954a) figures the palate. We have included new figures of the cavum pterygoidei of *Peltocephalus dumerilianus* to show the details of this structure.

*Neochelys* Bergounioux, 1954

SYNONYMY: See Broin (1977), Lapparent de Broin (2003a).

TYPE SPECIES: *Emys capelinii* de Zigno, 1889.

INCLUDED SPECIES: *Neochelys arenarum, N. fajumensis, N. franzeni, N. capellinii, N. eocenica, N. zamorensis.* See Broin (1977), Schleich (1993), and Lapparent de Broin (2003a) for more information on species.

DISTRIBUTION: Eocene, Europe, northern Africa. A possible podocnemidid record of a *Neochelys*-like epiplastron was reported by Hutchison et al. (2004). Although the epiplastron is very similar to some *Neochelys* we do not feel this is sufficient for a range extension to Southeast Asia. The epiplastron may not be a pleurodire.

DIAGNOSIS: A podocnemidid known from the skull and postcrania; skull relatively high and narrow in contrast to *Bauruemys*; orbits facing dorsolaterally; interorbital groove such as found in *Podocnemis* absent (except as a variation); temporal emargination less than in *Podocnemis*; parietal-quadratojugal contact long; cheek emargination slight; postorbital large in contrast to *Podocnemis*; medial expansion of triturating surface, median maxillary ridge, present; accessory ridge or ridges absent in triturating surface; vomer absent; fossa precolumellaris shallow as in *Podocnemis expansa* in contrast to deep as in *Erymnochelys*; foramen jugulare posterius

closed; interparietal scale equilateral triangle; cavum pterygoidei with large anterior opening and foramen cavernosum in roof; horizontal occipital shelf absent; chorda tympani enclosed in processus retroarticularis.

Postcrania with nuchal bone width greater than length; neural series variable with six or seven neurals extending to meet costals six and seven; first neural is four sided; axillary buttress reaches peripheral three; pectoral scales do and do not contact mesoplastra, but do contact entoplastron and epiplastra.

DISCUSSION: A number of species have been named for this genus, Broin (1977), Schleich (1993), and Lapparent de Broin (2003a) attempt to diagnose and clarify these. Only *Neochelys arenarum* Broin has had its skull described (except for the basisphenoid of *Neochelys* cf. *arenarum,* Lapparent de Broin, 2003a), although Lapparent de Broin (2003a: table 1) compares cranial features among *Neochelys arenarum* and some undescribed specimens.

Although the species are a problem, the genus is well diagnosed by a unique combination of characters. It possesses a wide parietal-pterygoid contact, as in the tribe Stereogenyini that is absent or narrow in *Podocnemis*, and absent in *Erymnochelys* and *Peltocephalus. Neochelys* has a relatively small interparietal scale that is an equilateral triangle, as in *Papoulemys* and some *Podocnemis,* but absent in *Erymnochelys, Peltocephalus,* and the tribe Stereogenyini. *Neochelys* and *Papoulemys* also lack accessory ridges in a group, the infrafamily Podocnemidodda, characterized by them.

Lapparent de Broin (2000a: 68; 2001: 171) questionably suggested the presence of *Neochelys* in the Fayum Eocene as "Genus indet. (*Neochelys* group?: '*Stereogenys*') *podocnemoides* Reinach, 1903: Qasr El Sagha beds, Fayum, Egypt Late Eocene" (Lapparent de Broin, 2000a: 68). Although there has not been further discussion of this suggestion, the known material of *podocnemoides* includes a plastron with a large intergular scale that divides the gulars, intergulars, and reaches the pectoral scales (Reinach, 1903: pl. 10, fig. 1), in contrast to the material identified in this paper as *fajumensis* (fig. 47), which has a small intergular not dividing these scales. Whether or not *podocnemoides* Reinach, 1903, belongs to *Neochelys* or another genus is indeterminable.

*Neochelys arenarum* Broin, 1977

TYPE SPECIMEN: MNHNP RI 45, a shell (Broin, 1977: text figs. 10–12; pl. 2, figs. 10, 11; see also for discussion and description).

TYPE LOCALITY: Rians, Var, France (Broin, 1977).

HORIZON: Sparnacian (Broin, 1977).

DIAGNOSIS: Broin (1977), Schleich (1993), and Lapparent de Broin (2003a) give diagnoses for the numerous European shell-based species and further references. Broin (1977: figs. 11, 12) shows the anterior plastral lobe of *arenarum* Broin, 1977, but with some individual variation, specimens all have the intergular scale separating the gular scales, in contrast to the condition in *fajumensis* Andrews, 1903, discussed below. Only *Neochelys arenarum* is known from a skull that has been described and it is very similar to that of *Neochelys fajumensis.*

REFERRED MATERIAL: Same data as type: MNHNP RI 6, nearly complete skull and jaws, slightly deformed, described and figured in Broin (1977: 70–83); MNHNP RI 7, probably not deformed but with few sutures visible; see list of other specimens in Broin (1977: 64); material from Rians, Var, France, in MDE: MDE R1 and MDE R2, skull and lower jaw.

PREVIOUS WORK: The skull of this species is well described and figured in Broin (1977). A disarticulated basisphenoid associated with other *Neochelys* fragments is described and figured in Lapparent de Broin (2003a). Schleich (1993) described a new species, *Neochelys franzeni*, with associated skull material, which is not described. Other known but undescribed *Neochelys* skulls (Jiménez Fuentes, 1988: 9, fig. 3; Lapparent de Broin, 2001: 170–171; 2003a: table 1) have been mentioned in the literature, but are apparently unavailable for study. The shell of *Neochelys arenarum* is described and figured in Broin (1977).

DISCUSSION: Although a number of species have been named, Broin (1977), Lapparent de Broin (2001), and some diagnosed comparatively in Broin (1977), Schleich (1993), and Lapparent de Broin (2003a), the

shell characters distinquishing the various species seem to be within the individual variation of many recent species of *Podocnemis,* in our assessment.

*Neochelys fajumensis* (Andrews, 1903), new combination

*Podocnemis fajumensis* Andrews, 1903.
*Podocnemis blanckenhorni* Reinach, 1903.
*Erymnochelys fajumensis* (Andrews) Lapparent de Broin, 2000a.

TYPE SPECIMEN: CGM 10202, anterior portion of plastron, collected by Beadnell, 1902, figured in Andrews (1903: pl. 8, fig. 2C; and Andrews, 1906: fig. 93) possibly now lost (Cyril Walker, R.C.W., unable to locate in Cairo Museum, personal commun.).

TYPE LOCALITY: "North of Birket-el-Qurun" Fayum Depression, Egypt (Andrews, 1906: 292).

TYPE HORIZON: "In the Upper Eocene beds remains of another small Pleurodiran are not uncommon" (Andrews, 1903: 121), who did not specifically designate a type locality or horizon. Later authors have reinterpreted the age assignment and concluded that *fajumensis* occurs only in the Oligocene part of the Jebel Qatrani Fm. (Simons, 1968; Seiffert, 2006, q.v. for further references). The age of the Jebel Qatrani Fm. is a complex question with current evidence supporting only the base of the Jebel Qatrani as Eocene (Seiffert, 2006). There is no direct evidence that any of the *N. fajumensis* material is Eocene, but as turtle distributions are frequently undocumented, this remains a possibility.

DIAGNOSIS: Six neurals, the first contacting nuchal; costals six, seven, eight meeting on midline; anterior end of nuchal very narrow, nuchal width-length about equal; intergular scale small, triangular or parallel sided, not completely separating gular scales, in contrast to all other *Neochelys,* or humeral scales on midline, barely extending onto entoplastron; differs from *"Podocnemis" podocnemoides* (von Reinach) in the gular and humeral scales meeting on the midline rather than being separated.

The shell is very similar to that of *Erymnochelys.*

ETYMOLOGY: Presumably for the Fayum, Egypt.

REFERRED MATERIAL: AMNH 5086 (fig. 86), anterior plastral lobe; AMNH 5093, anterior plastral lobe (fig. 86); AMNH 5087, carapace. Apparently, most of the AMNH specimens came from three quarries: A, B, and C, in the lower Fossil Wood zone of the Jebel Qatrani Fm. (Simons, 1968: 20; see also Moustafa, 1974, for map).

Similarly, the BMNH (including what was sent to Cairo and is now CGM) and YPM material are also probably from the early Oligocene part of the Jebel Qatrani Fm., according to Simons (1968: 19, 20). CGM 8790, shell; CGM 8509, anterior plastral lobe; BMNH R3103, anterior plastral lobe; BMNH R3435, anterior plastral lobe; YPM 6202, shell; YPM 6203, shell. The identifications are based almost entirely on the anterior plastral lobe morphology of the small intergular scale not separating the gulars or humerals.

We list all specimens found by the Duke parties because they provide evidence that the *Neochelys* skulls and jaws occur in close association with *fajumensis* shells in the Jebel Qatrani Fm. There is no documented case of an articulated set of cervicals connecting a skull with a shell, but the proximity of the skulls and shells is a matter of a few centimeters or less (D. Deblieux, E. Simons, personal obs.). Shell fragments of *fajumensis* are the commonest fossil in the Quarry L 41, Quarry M, and Quarry I localities, and only articulated shell material of some completeness was collected. Even the skeptical E.S.G. agrees that this skull-shell association should be accepted. Stratigraphic data for these quarries can be found in Bown and Kraus (1988: fig. 19, q.v. this paper for further references; see also Moustafa, 1974; Gingerich, 1992). The most recent age assessment for the Fayum stratigraphy (Seiffert, 2006) indicates that Quarry L-41 is ca. 35.4 Ma (latest Eocene), Quarries A, B, and C are ca. 34.8, and Quarries I, M, and P are ca. 30.2–29.5 Ma.

DPC 3146 (figs. 44, 45), skull, complete but lacking right temporal roof and cheek, right quadrate and squamosal, Quarry M, 82-1229; DPC 12143, laterally compressed skull, most elements present but considerably displaced by disarticulation, L-41, 92-461; DPC 15310, partial skull, most elements

present but considerably displaced by disarticulation, loss of palate and left quadrate and otic area, L-41, 95-350; DPC no number, L-41, 99-245 (fig. 46), nearly complete skull, dorsoventrally flattened and slightly disarticulated but not extensively deformed; DPC 1697, partial skull, consisting of both premaxillae, maxillae, frontals, partial parietals, postorbitals, jugals, palatines, and basisphenoid, Quarry I, 77-39; DPC 3882, skull lacking snout and skull roof, Quarry I, 83-252. These skulls listed above are from the Jebel Qatrani Fm., and are the basis (primarily DPC 3146) for the restorations in figures 42, 43.

DPC 6209, carapace, Quarry O, 86-861; DPC 2491, shell, Quarry R, 81-727; DPC 7747, shell, Quarry M, 85-986; DPC 9483, shell, Quarry I, 89-1028; DPC 4605, partial carapace, Quarry P, 83-1107; DPC 2149, disarticulated shell elements, Quarry M, 80-854; DPC 10686, shell, L-41, 90-936; DPC 10434, partial shell, L-41, 90-531.

All of the following are lower jaws and consist of the fused dentaries indistinguishable from the lower jaw of *Neochelys arenarum* Broin (1977: fig. 18, pl.2). DPC 1699, Quarry M, 77-240; DPC 2003, Quarry I, 80-813; DPC 2223, Quarry M, 80, 311; DPC 2230, Quarry M, 80-345; DPC 2602, Quarry M, 81-586; DPC 2747, Quarry M, 81-137; DPC 2754, Quarry M, 81-176; DPC 2779, Quarry P, 81-52; DPC 2858, Quarry M, 81-563; DPC 3249, Quarry I, 82-623; DPC 3261, Quarry M, 82-542; DPC 3261, Quarry M, 82-542; DPC 3308, Quarry M, 82-542; DPC 3308, Quarry I, 82-161; DPC 3442, Quarry M, 82-951; DPC 3862, Quarry M, 83-464; DPC 3973, Quarry M, 83-431; DPC 4291, Quarry M, 83-1380; DPC 4400, Quarry M, 83-302; DPC 4413, Quarry M, 83-123; DPC 4495, Quarry M, 83-787; DPC 5068, Quarry M, 84-825; DPC 5193, Quarry I, 84-867; DPC 5520, Quarry M, 85-990; DPC 5749, Quarry M, 85-193; DPC 5786, Quarry I, 85-141; DPC 5892, Quarry M, 85-309; DPC 6205, two lower jaws, Quarry M, 86-933; DPC 6413, Quarry M, 86-336; DPC 6522, Quarry M, 86-95; DPC 6558, Quarry M, 86-332; DPC 7331, Quarry M, 87-300; DPC 7545, Quarry M, 87-758; DPC 7546, Quarry I, 87-780; DPC 7673, Quarry I, 87-859; DPC 9352A, Quarry M, 89-384; DPC 9795, Quarry M, 89-330; DPC 10226, Quarry I, 90-107; DPC 10382, Quarry I, 90-347; DPC 10607, Quarry M, 90-1208; DPC 11192, two lower jaws, Quarry M, 91-362; DPC 11403, Quarry M, 91-780; DPC 12116, Quarry M, 92-407.

DISCUSSION: The identification of *Neochelys* in the Fayum extends the range of this genus outside Europe to North Africa. The skull material from the Egyptian early Oligocene units is hardly distinguishable from the European Eocene *Neochelys*. However, the identification of this material with the Oligocene species *fajumensis*, extends the temporal range of *Neochelys*, formerly known from the early to late Eocene of Europe (55–34 Ma), adding approximately another 5 Ma to the already long duration of this genus. The recognition of *Neochelys* in the Paleogene of North Africa also adds another piece to the biogeographic puzzle of Afro-European dispersal in the Paleogene (Lapparent de Broin, 2003a).

The recognition of *fajumensis* as *Neochelys* is based not only on the hypothesis that the shells and skulls in the Duke quarries are associated, which is testable but not certain, but that the characters used to diagnose *fajumensis* actually are restricted to this single species. It is possible that these characters diagnose a wider group of taxa, as the shell characters in the Pelomedusoides (particularly the Podocnemididae), tend to be conservative in comparison to the skulls (discussion above and in Gaffney et al., 2006). Furthermore, *fajumensis* (fig. 47) and the Duke material differ from all European *Neochelys* in having small intergular scales allowing the gular scales to contact on the midline. The anterior lobe in the Pelomedusoides is the most variable part of the shell and has figured prominently in pleurodire shell taxonomy. Unfortunately, it is also individually variable (E.S.G., P.A.M., R.C.W., personal obs.), and too much emphasis has been placed on this area for characters in our judgements. Even Andrews (1906) showed that there was variation in the anterior plastral lobe of his podocnemidids.

We conclude that there are no systematic differences between the shells in the Duke quarries associated with skulls of *Neochelys,*

and the shells identified in the literature as *fajumensis.* One could still argue that this taxon is not *Neochelys* because all *Neochelys* known to date have the intergular scales separating the gular scales. But then one would have to argue either that the skulls are not *Neochelys* or that they are not associated with the shells.

The synonymy of *Podocnemis blanckenhorni* Reinach, 1903, with *Podocnemis fajumensis* Andrews, 1903, appears to be correct, but the synonymy with *Dacquemys* suggested by Williams (1954c) is clearly not. The proposed synonymy of *Pelomedusa progaleata* Reinach, 1903, with *fajumensis* (Lapparent de Broin, 2000a) is hard to support as the type material is inadequate for useful comparison. *Pelomedusa progaleata* Reinach, 1903, is better considered as a nomen dubium.

DESCRIPTION OF THE SKULL: The description of the skull of *Neochelys arenarum* by Broin (1977) is extremely close to the Egyptian skulls and only differences are noted below. Our description is based mostly on DPC 3146 (figs. 42–45) with some information from DPC 99-245 and other cranial fragments listed above.

The skull figured by Broin, MNHNP RI 6 (1977: figs. 13–18, pl. 2), is one of a series available for this species. All of the skulls in the series are slightly deformed, and the figured skull is slightly wider and lower than the others, which are narrower and almost exactly the same shape as DPC 3146, particularly the apparently undeformed MNHNP RI 7. So the wide shape of the figured *Neochelys arenarum* seems to be due to preservation and is unique to that specimen.

The prefrontal-frontal suture in the Egyptian specimens is W-shaped in dorsal view (fig. 42) and in MNHNP RI 6 it is transverse. DPC 3146 has an interorbital groove, similar to that seen in *Podocnemis,* but with a much wider interorbital distance. The other Egyptian skulls, however, do not show this groove, although we have coded *Neochelys* as present and absent for this character. DPC 3146 has a more emarginate posterior temporal roof with a greater quadratojugal exposure along the edge than in *Neochelys arenarum*, but this is within the range of variation frequently seen in many turtles. What may be the only significant distinction between the Egyptian skulls and the *Neochelys arenarum* series is in the cheek. The quadratojugal in DPC 3146 has a greater exposure along the cheek emargination than in MNHNP RI 6 associated with a smaller anterior process of the quadrate. It is possible, however, that even this is due to breakage in DPC 3146. In any case, we have not seen consistent characters that would differentiate the French *Neochelys* skulls from the Egyptian *Neochelys* skulls. They would probably be placed in the same species, if only the skulls were known.

DESCRIPTION OF THE SHELL: The reconstruction of the shell of *Neochelys fajumensis* (fig. 47) is based on a number of specimens: YPM 6202, AMNH 5087, CGM 8790, CGM 10202, AMNH 5086, AMNH 5093, CGM 8509, BMNH R3103, BMNH R3435, and YPM 6203.

The carapace of *Neochelys fajumensis* is domed and oval in the uncrushed examples in both groups; there are eight costals and 11 peripherals. Peripherals 8–11 and the pygal (YPM 6203 and CGM 8690) bear a ridge on their inner surface, which can also be seen in DPC 2491, DPC 7747, DPC 2225 and DPC 9483. The nuchal is wider than long, with an unusually narrow anterior half, in both groups of specimens. The first neural is four sided, as in most pleurodires. There are either five (YPM 6202, AMNH 5087, CGM 8790), six (DPC 2491), or seven (DPC 6209, DPC 7747) neural bones. This is accompanied by either costals six to eight meeting on the midline or just costals seven and eight meeting on the midline.

The plastron of *Neochelys fajumensis* has an anterior lobe that is shorter than the posterior lobe and is squared off along its anterior margin. Small swellings are present marking each of the scale areas: intergular, gular, and humeral. The outer border of the posterior lobe curves medially in a gentle arc to the tips of the xiphiplastra. The entoplastron varies slightly from all four sutures being straight to having the posterior pair curved; their margin convex posteriorly. Mesoplastra are preserved in CGM 8790, DPC 2491, and DPC 7747. There is no sulcus on the mesoplastron. The anal notch varies from wide and semicircular to narrower and more

V-shaped. On the inner surface of the posterior lobe, along the lateral margin just inside the body wall attachment ridge is a low ridge of thickened bone paralleling the margin. Narrow intergular scales not completely separating the gular scales is one of the diagnostic features used in the literature for "*Podocnemis*" *fajumensis*.

### *Papoulemys* Tong, 1998

*Neochelys laurenti* (Tong) Lapparent de Broin, 2001

TYPE SPECIES: *Papoulemys laurenti* Tong, 1998.

INCLUDED SPECIES: *Papoulemys laurenti.*

DISTRIBUTION: Early Eocene of France.

DIAGNOSIS: A podocnemidid known from the skull; skull relatively high and narrow in contrast to *Bauruemys*; orbits facing dorsolaterally; interorbital groove such as found in *Podocnemis* absent; temporal emargination less than in *Podocnemis*; parietal-quadratojugal contact long; cheek emargination slight; postorbital large in contrast to *Podocnemis*; medial expansion of triturating surface, median maxillary ridge, present; accessory ridge or ridges absent in triturating surface as in *Neochelys*; fossa precolumellaris present but shallow as in *Podocnemis expansa* in contrast to deep as in *Erymnochelys*; foramen jugulare posterius closed; interparietal scale small equilateral triangle as in *Neochelys*; horizontal occipital shelf absent; differs from *Neochelys* in condylus occipitalis consisting mostly of exoccipitals, quadratojugal exposure on cheek wider.

DISCUSSION: Lapparent de Broin (2001: 170) considers this genus a species of *Neochelys*. Considering the large number of common characters, this is a reasonable interpretation. There are differentiating characters, however, and as the other known *Neochelys* skulls (Jiménez Fuentes, 1988: fig. 3; Lapparent de Broin, 2001: 170–171; 2003a: table 1) have so far not been described or figured with sutures, it is hard to judge what the diagnostic skull characters for the European species of *Neochelys* might be. Therefore, we keep *Papoulemys* and find it to come out in a trichotomy with *Neochelys* and the tribe Stereogenyini. It is possible that a revision of *Neochelys* using the now available skull material (including *N. fajumensis*) would place *laurenti* in that genus.

### *Papoulemys laurenti* Tong, 1998

TYPE SPECIMEN: Musée des Dinosaures, Esperaza, France, T12.

TYPE LOCALITY: Saint-Papoul, Aude, France.

HORIZON: Cuisian, early Eocene.

DIAGNOSIS: As for genus.

PREVIOUS WORK: Tong (1998), Lapparent de Broin (2001).

### Tribe Stereogenyini, new

DIAGNOSIS: Members of the Podocnemididae; dorsal process of palatine reaches frontal in side wall of braincase; fossa precolumellaris absent; both foramina nervi hypoglossi combined and recessed in a short canal opening on occipital surface.

INCLUDED TAXA: *Bairdemys* Gaffney and Wood, 2002; *Shweboemys* Swinton, 1939; *Stereogenys* Andrews, 1901; *Mogharemys,* n. gen.; *Cordichelys,* n. gen.; *Latentemys,* n. gen.; *Brontochelys,* n. gen.; *Lemurchelys,* n. gen.

DISCUSSION: There should be a coordinate tribe-level taxon for Stereogenyini, and according to the analysis presented here (fig. 98), it would be *Neochelys* + *Papoulemys* (or *Erymnochelys* + *Peltocephalus* if one were just considering the recent fauna). However, as discussed elsewhere (Phylogenetic Analysis) the resolution in this part of the magnatribe Erymnochelydand is not well supported for some taxa. Therefore, we are avoiding the formal recognition of a tribe for the sister taxon to Stereogenyini, but it's probably *Neochelys*.

### Subtribe Mogharemydina, new

DIAGNOSIS: As for genus *Mogharemys.*

INCLUDED TAXA: *Mogharemys,* n. gen.

### ***Mogharemys,*** new genus

TYPE SPECIES: *Sternothaerus blanckenhorni* Dacqué, 1912.

INCLUDED SPECIES: *Mogharemys blanckenhorni.*

DISTRIBUTION: Miocene of Egypt.

DIAGNOSIS: A podocnemidid of the Tribe Stereogenyini known only from the skull,

uniquely possessing a median maxillary ridge on palatine smaller than lateral maxillary ridge; secondary palate and midline palatal cleft absent, medially expanded triturating surfaces not meeting on midline; orbits facing more anteriorly than laterally as in *Bairdemys venezuelensis*; eustachian tube confluent with fenestra postotica; parietal-pterygoid contact in septum orbitotemporale as in Tribe Stereogenyini and in contrast to *Erymnochelys, Peltocephalus*, and *Podocnemis*; dorsal process of palatine reaches ventral process of frontal as in Tribe Stereogenyini and in contrast to all other podocnemidids; posterior pocket of fossa orbitalis as found in Tribe Stereogenyini absent; fossa precolumellaris absent as in all Tribe Stereogenyini and in contrast to *Erymnochelys, Peltocephalus*, and *Podocnemis*; foramina nervi hypoglossi combined into one recessed opening posteriorly as in Tribe Stereogenyini.

Discussion: This new genus is based on a skull in the British Museum, BMNH R.8440 (figs. 48–51) that was described but not named, by Williams (1954), who did not realize that the skull was the holotype of "*Sternothaerus" blanckenhorni* Dacqué, 1912. Williams listed characters showing BMNH R.8440 to be distinct from all other podocnemidid skulls, but refrained from naming it because he thought it was probably the skull of the shell-based taxon "*Podocnemis" aegyptica* Andrews, 1900, which Williams stated (1954: 5) "is on shell characters barely, if at all, distinguishable from *Erymnochelys madagascariensis*." Williams hypothesized that the Moghara skull, BMNH R.8440, was "a structural intermediate between the Recent genera, *Peltocephalus* or *Erymnochelys,* and the Oligocene *Dacquemys*" (Williams, 1954: 6). Williams also suggested that BMNH R.8440 could be the skull of the other Moghara shell, *Podocnemis bramlyi*, but did not decide in favor of either hypothesis.

Williams discussed *"Sternothaerus" blanckenhorni,* the only other Moghara skull known at that time. He felt the sole figure of the specimen, a dorsal view (Dacqué, 1912: fig. 12) neither supported nor contradicted the assignment to *Pelusios* (= *Sternothaerus*). However, Williams was misled by the written description of Dacqué (1912: 321), that "*Sternothaerus*" *blanckenhorni* was characterized by a strongly developed secondary palate, which does not occur in BMNH R.8440. No other figures of "*Sternothaerus*" *blanckenhorni,* showing the ventral view, for example, have appeared or were available to Williams, although the cast, MB.R.2860, was in the Berlin Museum at this time. Williams was aware that the Egyptian Tertiary had podocnemidids, such as *Stereogenys,* with well-developed secondary palates and concluded that "*Sternothaerus*" *blanckenhorni* could be one of these, but, in any case, a secondary palate is not present in BMNH R.8440. BMNH R.8440 has an expanded triturating surface compared with the living podocnemidids, which was apparently all that Dacqué meant, but it was not expanded to the extent seen in *Stereogenys.*

A recent examination by E.S.G. of the cast of "*Sternothaerus*" *blanckenhorni* Dacqué, 1912, MB.R.2860, in the Berlin Museum shows that the original of the cast is actually BMNH R.8440. In ventral view the comparisons are exact, even though some of the cast does not preserve surface details. The actual specimen, BMNH R.8440, has lost the prefrontals and some chips from the edges of the skull, so the dorsal view is now significantly different from the 1912 figure. When Dacqué examined the specimen it was in the collection of the Geological Survey of Egypt (Dacqué, 1912: 321); exactly how it came to be at the BMNH is unknown. The reconstruction of the skull produced here (fig. 48) combines both the original specimen and the missing snout features from the cast.

### ***Mogharemys*** *blanckenhorni* Dacqué (1912), new combination

*Sternothaerus blanckenhorni* Dacqué, 1912
*Pelusios blanckenhorni* Williams, 1954

Type Specimen: BMNH R.8440, the holotype of "*Sternothaerus*" *blanckenhorni* Dacqué, 1912, is a partial skull in two pieces, not in contact. Dacqué did not specifically designate a type, and the only specimen he figured was the cast of this skull. However, it is apparent that he considered the skull the type specimen, and we affirm that. Dacqué (1912: 321) mentions shell fragments associated with the skull. What seem to be these

specimens was examined by one of us (R.C.W.) and found to be too fragmentary to support Dacqué's original identifications. They were not figured.

TYPE LOCALITY: "Wadi Moghara" label (see Miller, 1999).

HORIZON: Unnamed formation, Miocene. "untermiocänen Eisensandstein von Moghara: die Knochenplatten aus derselben Stufe in Wadi Faregh" (Dacqué, 1912: 321).

DIAGNOSIS: As for genus.

ETYMOLOGY: For the locality, Wadi Moghara, Egypt, and *emys,* Greek for "freshwater tortoise."

REFERRED MATERIAL: MB.R.2860, a cast of BMNH R.8440, made before damage resulting in the loss of the snout occurred, figured in Dacqué (1912: fig. 12).

PREVIOUS WORK: See below.

DISCUSSION: The species name *blanckenhorni,* has been used by two different authors for two different species with two different type specimens. Both specimens are podocnemidids from the same area, the Fayum of Egypt, but from slightly different ages and different localities. Professor M. Blanckenhorn was a German geologist who worked in Egypt for many years (Blanckenhorn, 1900, 1903, 1921) and was particularly active in collecting in the Moghara area (Andrews, 1906), and apparently popular.

The older *blanckenhorni* was named by von Reinach in 1903 (1903a) and consisted of the anterior half of a plastron, at that time housed in the Munich Museum, and which was probably destroyed in World War II (Crumly, 1984). Named "*Podocnemis*" *blanckenhorni* by Reinach (1903a: 460), Reinach also named it in Reinach (1903b: 27; the present authors do not know which publication was first, so we use the lettering from Kuhn, 1964). Andrews (1906: 292) suggested that "*Podocnemis*" *blanckenhorni* was a junior synonym of *"Podocnemis" fajumensis* Andrews, 1903, and we have accepted that.

In 1912, Dacqué used the species name for "*Sternothaerus*" *blanckenhorni,* the specimen named here *Mogharemys blanckenhorni* (Dacqué). It was Kuhn (1964) who confused *blanckenhorni* Reinach, 1903a and 1903b, with *blanckenhorni* Dacqué, 1912, and put them into synonymy. Lapparent de Broin (2000a) clearly differentiated the two species.

All of this may be moot, as the commonest shell in the Moghara unit according to Andrews (1900: 2), belongs to "*Podocnemis*" *aegyptica* Andrews, 1900 (fig. 87). Perhaps someday a skull-shell association may allow a new assessment of the taxonomy of BMNH R.8440.

### Subtribe Stereogenyina, new

DIAGNOSIS: Members of the Podocnemididae; secondary palate unique among turtles in being formed by maxillae and palatines that are separated on the midline by a narrow cleft; median maxillary ridge of other Podocnemididae absent; palate characterized by variably developed anterior convexity and posterior concavity; palatine makes up half or more of secondary palate; fossa orbitalis with extensive posterior pocket behind orbital rim enclosed by septum orbitotemporale.

INCLUDED TAXA: *Bairdemys* Gaffney and Wood, 2002; *Shweboemys* Swinton, 1939; *Stereogenys* Andrews, 1901; *Cordichelys,* n. gen.; *Latentemys,* n. gen.; *Brontochelys,* n. gen.; *Lemurchelys,* n. gen.

### Infratribe Bairdemydita, new

DIAGNOSIS: Members of the Subtribe Stereogenyina; cheek emargination present; labial ridge high and narrow; angle of front of skull is 90° or less, in contrast to the Infratribe Stereogenyita in which it exceeds 90°; pinched snout absent (slightly developed in *Bairdemys hartsteini* and approached by *Bairdemys winkleri*).

INCLUDED TAXA: *Bairdemys* Gaffney and Wood, 2002; *Cordichelys,* n. gen.; *Latentemys,* n. gen.

DISCUSSION: The other clade coordinate with this one is the Infratribe Stereogenyita, which has no cheek emargination. There is, however, a serious problem with this character as only one specimen in this subtribe is determinable (a *Stereogenys*); the other three genera lack preserved cheeks. However, the two clades are also distinguishable by the labial ridge, which is low and thick in the Stereogenyita and high and thin in the Bairdemydita, the primitive condition. The angle of the snout is somewhat arbitrary, and the identification of what is a pinched snout and what is not has varied in the literature

(Gaffney and Wood, 2002; Sánchez-Villagra and Winkler, 2006; Gaffney et al., 2008).

***Cordichelys,*** new genus

TYPE SPECIES: *Podocnemis antiqua* Andrews, 1903.

INCLUDED SPECIES: *Cordichelys antiqua.*

DIAGNOSIS: A podocnemidid of the Tribe Stereogenyini known from the skull and shell; uniquely possessing among the Tribe Stereogenyini a cordiform (heart-shaped) carapace, shallow interorbital depression, pterygoids narrowly meeting on midline in contrast to either not meeting (*Shweboemys* and *Stereogenys*) or broadly meeting (all other Tribe Stereogenyini), a large ventral process of the postorbital in the septum orbitotemporale contacting palatine and preventing jugal-pterygoid contact; medial edges of palatal cleft curved in contrast to *Lemurchelys, Shweboemys,* and *Stereogenys*; low ventral convexity on triturating surface in contrast to high in *Bairdemys*; eustachian tube confluent with fenestra postoticum; antrum postoticum open as in *Latentemys* in contrast to nearly closed in *Bairdemys*; frontal and prefrontal flat in profile as in *Shweboemys* in contrast to rounded in *Bairdemys.*

Postcrania with six neurals extending to costals six; first neural four sided; pectoral scales do not contact mesoplastra, but do contact entoplastron and epiplastra.

DISTRIBUTION: Egypt, late Eocene.

INCLUDED SPECIES: *Cordichelys antiqua.*

ETYMOLOGY: *Cordi-*, from Latin *cor,* "heart," in allusion to heart-shaped carapace; *chelys*, Greek "turtle."

DISCUSSION: *Cordichelys* resolves as the sister taxon to the remaining members of the Infratribe Bairdemydita, but the number of supporting characters is not great. *Cordichelys* and *Latentemys* are relatively generalized within the Tribe Stereogenyini.

***Cordichelys*** *antiqua* (Andrews, 1903), n. gen.

*Podocnemis antiqua* Andrews, 1903
*Podocnemis stromeri* Reinach, 1903a
*Shweboemys antiqua* Wood, 1970
*Stereogenys cromeri* Andrews, 1906 (in part)
"*Pod. Stromeri* var. *major*," Reinach, 1903a

TYPE SPECIMEN: CGM 10038 (Andrews, 1903: pl. 8, figs. A, B; more detailed description with same figure in Andrews, 1906), a nearly complete shell so heavily coated with gypsum that none of the scute sulci and only some of the bone sutures can be recognized.

TYPE LOCALITY: "north of Birket el-Qurun" Andrews (1906: 289).

TYPE HORIZON: "Qasr el-Sagha beds (Middle Eocene)...." Andrews (1906: 289); now regarded as late Eocene (Holroyd et al., 1996; Seiffert, 2006).

DIAGNOSIS: Genus is monotypic.

REFERRED SPECIMEN: YPM 7457 (formerly YPM 6205; field number 67-502, accession 7152; skull drawings published by Gaffney, 1979: fig. 136 as YPM 6205), associated skull and shell (figs. 53–57); "Eocene, Qasr el-Sagha Fm., Zeuglodon Valley, Egypt, collected Lloyd Tanner, 1966–67" (label and YPM database, original accession data states only "Zeuglodon Valley"). According to P. Holroyd (personal commun.) the Qasr el-Sagha Fm. does not outcrop in Zeuglodon Valley and the source is more likely the Birket Qarun Fm. However, Moustafa (1974: fig. 4) shows a "*Podocnemis antiqua*" partial shell in situ in the Qasr el-Sagha Fm. that may be YPM 7457 (P. Holroyd, personal commun.).

DISCUSSION: Considering the large number of commonly shared characters evident in the shells of *Cordichelys antiqua* and "*Podocnemis stromeri,*" i.e., the pointed xiphiplastra, straight outer borders of the posterior plastral lobe, short anterior plastral lobe, indentation at the front end of the carapace, same number of neurals, and in general the similar configurations of bone sutures and scute sulci; it seems reasonable to conclude that all these specimens belong to a single species. Therefore, we have synonymized "*Podocnemis stromeri*" Reinach, 1903a, including "*Pod. Stromeri* var. *major*," with *Cordichelys antiqua.*

DESCRIPTION: Although the type specimen of "*Podocnemis*" *antiqua* (CGM 10038) consists of a fairly complete shell, it is so heavily coated with gypsum that none of the scute sulci and only some of the bone sutures can be recognized. The Yale specimen (YPM 7457, figs. 56, 57), which forms the basis for the following description, now permits a much fuller account to be given of the shell

of this poorly known species as well as of its skull.

Andrews (1906: 289) commented regarding the type of "*Podocnemis*" *antiqua* that: "The carapace in this species is flatter posteriorly than in front, where it seems to have been highly arched. The nuchal border is straight, without a trace of any emargination." Crushed bone may have misled Andrews in reconstructing the only specimen he had available for study. Inspection of the Yale specimen confirms only part of this description. The entire carapace was apparently rather flat and more or less low arched in cross section. No evidence of a more pronounced arching toward the front can be detected in the Yale specimen. In addition, a definite emargination in the anterior edge of the nuchal is clearly discernible, producing an unusual cordiform shell.

Eleven peripherals that extend along either side of the carapace from the nuchal back to the pygal are preserved on one side or the other of YPM 7457. Contrary to Andrew's observation (1906: 290) that "The last marginals [peripheral bones] and pygals are somewhat enlarged," these elements appear to be roughly equivalent in size to the anterior peripherals, and it would appear that the middle peripherals in the series are actually the largest. Numbers seven, eight, and nine are larger than the others, being not only longer but also wider than the others. The nuchal is much wider than long and, as noted above, is indented along the anterior margin. Andrews (1906: 289) mentioned that "at the point of junction of the nuchal, first neural, and first costal there is a small opening through the shell." Apparently he regarded this as a natural fenestration. No similar structure is evident on the Yale specimen, and in view of the poor state of preservation of the type it is reasonable to assume that the holes that Andrews observed can be attributed to distortion caused by crushing. Six neurals are present, the first one abutting directly against the posterior end of the nuchal. The first neural is fusiform in shape, while the following four are hexagonal and elongate anteroposteriorly. The last neural is pentagonal in outline and as wide as it is long. Intervening between the last neural and the suprapygal are three costals (numbers six, seven, and eight) that meet in the midline. Of the eight costals, the first is the largest and there is a progressive decrease in size posteriorly. The suprapygal is pentagonal, its borders abutting against the last pair of costals, the 11th pair of peripherals, and the pygal. In typical pleurodiran fashion, the pelvic girdle was fused to the carapace and plastron. However, because of severe weathering in the area of the iliac attachment, it is not possible to determine the outline of the scars representing the point of fusion between pelvis and carapace.

There are five vertebral scales, all roughly hexagonal in outline. The first is slightly wider at its widest point than the nuchal bone underlying it. It converges anteriorly and is narrower than the nuchal where it reaches the anterior margin of the shell. This species is unique among Pelomedusoides in that the first vertebral extended forward to the anterior margin of the carapace, preventing the first pair of marginal scales from meeting in the midline (fig. 56). Four pairs of pleural scales are arranged along either side of the vertebrals. Extending around the fringe of the carapace are 12 marginal scales. The first pair do not meet at the front of the shell, as noted above, because of the interposition of the first vertebral scale. The sulci between the pleurals and marginals are situated well down on the peripheral bones, more or less midway between their distal and proximal ends.

In the plastron of the type, the scale sulci are unrecognizable, and the pattern of bone sutures on the outer surface is obscured. What Andrews (1906: 290) described was actually the bone suture pattern on the inner surface of the plastron. The Yale shell (YPM 7457) confirms his general description, however. The posterior lobe of the plastron is narrower than the anterior one, and it extends much farther from the bridge than does the anterior lobe. The exterior surface of the plastron is completely flat except for a slight upward curve at the posterior tip of the acutely pointed xiphiplastra. Situated rather more anteriorly than in most other pleurodires, the diamond-shaped entoplastron permits only a narrow contact between the epiplastra at the anterior margin of the plastron. From the outer angles of the entoplastron, sutures separating the epiplas-

tra from the hyoplastra extend to the outer border on a line approximately perpendicular to the long axis of the shell. The complex pattern of these sutures, which Andrews described, is characteristic only of the inner surface of the plastron. The sutures between the hyoplastra and hypoplastra bisect the middle of the bridge and terminate laterally in a junction with the mesoplastral sutures. No mesoplastra have been preserved, but from the notch between the lateral borders of the hyo- and hypoplastron it is possible to determine that they were relatively small and probably hexagonal. The suture between the hypoplastra and the xiphiplastra is situated about one-third of the distance from the posterior end of the bridge to the posterior end of the plastron. A V-shaped notch is excavated into the posterior border of the xiphiplastra. The relative position and orientation of the ischial and pubic scars are not very different from those of recent specimens of *Pelusios*, *Pelomedusa*, and *Podocnemis*. Possibly, however, in *Cordichelys antiqua* the ischial scar may be relatively larger than the pubic scar as compared to the living forms. The pelvis itself has not been preserved.

Interposed between the gulars is a narrow triangular intergular that extends posteriorly onto the entoplastron and separates the small triangular gulars at the midline. Along the posterior part of their midline borders, the humerals meet each other, but anteriorly they too are separated by the intergular. For the most part, the lateral portions of the humeropectoral sulcus coincide with the epi-hyoplastral suture. The pectoral-abdominal sulcus does not cross the mesoplastra; the position of this and the remaining plastral sulci are indicated in figure 56.

### ***Latentemys,*** new genus

TYPE SPECIES: *Latentemys plowdeni,* new species.

INCLUDED SPECIES: *Latentemys plowdeni.*

DIAGNOSIS: A podocnemidid of the Tribe Stereogenyini known only from the skull; uniquely possessing large, oval orbits, with widest dimension dorsally; medial edges of palatal cleft curved in contrast to *Lemurchelys, Shweboemys,* and *Stereogenys*; low ventral convexity on triturating surface in contrast to high in *Bairdemys*; eustachian tube separated from rest of fenestra postotica as in *Bairdemys* and in contrast to *Cordichelys*; antrum postoticum open in contrast to nearly closed as in *Bairdemys*; frontal and prefrontal slightly curved in profile as in *Brontochelys* and in contrast to *Shweboemys*; jugal-pterygoid contact present due to absence of ventral process of postorbital in septum orbitotemporale in contrast to *Cordichelys*; basisphenoid relatively short in contrast to other Infratribe Bairdemydita; large cavum pterygoidei prevents quadrate-pterygoid contact posteriorly in contrast to *Cordichelys* and *Bairdemys.*

DISTRIBUTION: ?Egypt.

ETYMOLOGY: *Latent*, from Latin *latens, -entis,* "hidden," in allusion to the indeterminant locality data; *emys*, Greek "freshwater tortoise."

### ***Latentemys plowdeni,*** new species

TYPE SPECIMEN: BMNH R.11998, a nearly complete skull (figs. 58–61). Collected by W. Plowden.

TYPE LOCALITY AND HORIZON: Probably Egypt, probably Tertiary, possibly Miocene. The specimen was donated to the BMNH by W. Plowden, who obtained it in Egypt during military service. The dark brown, loose matrix type of preservation suggests the Moghara Fm. rather than Eocene-Oligocene sediments.

DIAGNOSIS: Genus is monotypic.

ETYMOLOGY: In recognition of the presumed collector, W. Plowden.

DISCUSSION: *Latentemys* is the sister taxon to *Bairdemys* in our resolution of the characters. But the position of both *Latentemys* and *Cordichelys* are relatively poorly supported in this cladogram (s. 98, 99).

### *Bairdemys* Gaffney and Wood, 2002

TYPE SPECIES: *Bairdemys hartsteini* Gaffney and Wood, 2002.

INCLUDED SPECIES: *Bairdemys hartsteini, B. venezuelensis, B. sanchezi, B. winklerae.* AMNH 30000, an unnamed skull from the Castillo Formation, is considered as another species of *Bairdemys* (see below).

DIAGNOSIS: A podocnemidid of the Tribe Stereogenyini known from the skull and shell; uniquely possessing among the Tribe Stereogenyini an extremely small and slitlike postotic antrum, and a ventral vertical flange on the squamosal; medial edges of palatal cleft curved in contrast to *Lemurchelys, Shweboemys,* and *Stereogenys*; eustachian tube separated by bone from rest of fenestra postotica as in *Latentemys* but in contrast to all other Tribe Stereogenyini; jugal-pterygoid contact present in contrast to *Cordichelys, Shweboemys,* and *Stereogenys*.

Postcrania with saddle-shaped cervicals (known only for *B. hartsteini*); carapace (known only for *B. venezuelensis*) lacking neurals, costals meeting on midline; anterior plastral lobe short in contrast to nearly all other Podocnemididae; pectoral-abdominal sulcus not crossing mesoplastron; pectoral-humeral sulcus in anterior half of entoplastron; intergular scales barely extending onto entoplastron.

DISTRIBUTION: Miocene of Puerto Rico and Venezuela. Weems (2009) has described the shell and lower jaws of a *Bairdemys* from the Oligocene of South Carolina, thus extending the range of this genus. Weems also hypothesized that partial shell remains from the Miocene of Cuba (MacPhee et al., 2003) and the Miocene of Maryland (Collins and Lynn, 1936) are *Bairdemys,* but this material is too incomplete to confirm.

### *Bairdemys hartsteini* Gaffney and Wood, 2002

TYPE SPECIMEN: AMNH 27222, a skull without associated mandible figured by Gaffney and Wood (2002).

TYPE LOCALITY: North side of Highway No. 2, west of Bayamon, Puerto Rico (see Gaffney and Wood, 2002: 4).

HORIZON: Cibao Formation, middle Miocene (see Gaffney and Wood, 2002: 4).

DIAGNOSIS: A species of *Bairdemys* differing from all other species in having a higher skull, a straight rather than convex or concave labial ridge in ventral view, and a wider distance between orbits; also differs from *B. venezuelensis* in having a smaller skull, a premaxillary notch, lower triturating surface convexity, shallower triturating surface concavity, and narrower posterior triturating surface width; also differs from *B. sanchezi* in having a slightly wider skull, a higher triturating surface convexity, a deeper triturating surface concavity, a larger and broader basisphenoid, and a less extensive cheek and temporal emargination; also differs from *B. winklerae* in having a broader, shorter snout, slightly wider skull, wider triturating surface, a premaxillary notch, and a narrower basisphenoid-quadrate contact.

REFERRED MATERIAL: None.

PREVIOUS WORK: Gaffney and Wood (2002), Sánchez-Villagra and Winkler (2006), and Gaffney et al. (2008).

DISCUSSION: This species is not well differentiated from *B. venezuelensis*, and another option for grouping the *Bairdemys* species would be to synonymize *B. hartsteini* with *B. venezuelensis* but to keep *B. sanchezi* and *B. winklerae,* which are more distinct. Although the size range of Urumaco skulls of *B. venezuelensis* has been expanded, this species continues to differ from *B. venezuelensis* in its smaller size.

### *Bairdemys venezuelensis* (Wood and Díaz de Gamero, 1971)

TYPE SPECIMEN: Laboratorio de Paleontología, Universidad Central de Venezuela (Caracas), VF 1176, a complete carapace figured by Wood and Díaz de Gamero (1971: pls. 1, 2, 4).

TYPE LOCALITY: "North of Campo El Mamón, state of Falcón, Venezuela" (Wood and Díaz de Gamero, 1971).

HORIZON: Late Miocene, Urumaco Formation.

DIAGNOSIS: A species of *Bairdemys* differing from all other species in having a higher anterior triturating surface convexity, a deeper posterior triturating surface concavity, and a short midline contact of the pterygoids; also differs from *B. hartsteini* in having a larger skull, a convex labial ridge in ventral view, no premaxillary notch, and a wider posterior triturating surface; also differs from *B. sanchezi* in having a wider skull, a wider posterior triturating surface, a larger basisphenoid, no premaxillary notch, and a less extensive cheek and temporal emargination; also differs from *B. winklerae* in having

a broad, convex, and short snout, a slightly wider skull, a wider posterior triturating surface, and a narrower basisphenoid-quadrate contact.

ETYMOLOGY: For the country of Venezuela.

REFERRED MATERIAL: See list in Gaffney and Wood (2002).

PREVIOUS WORK: Wood and Díaz de Gamero (1971), Gaffney and Wood (2002), Sánchez-Villagra and Winkler (2006), Gaffney et al. (2008), Sánchez-Villagra and Scheyer (2010). Winkler and Sánchez-Villagra (2006) describe eggs from a likely *Bairdemys venezuelensis* nesting site, indicating that it was a colonial nester laying its eggs in beaches and living in a marine or near shore marine environment. Sánchez-Villagra and Scheyer (2010) provide a useful overview of the Venezuelan fossil turtles.

DISCUSSION: Although this is the oldest named species in the currently construed genus *Bairdemys*, the type species is *hartsteini*, named by Gaffney and Wood (2002) so that the genus had a skull as its type species, in case some or all of the shell features of *B. venezuelensis* prove to be taxonomically widespread, as is in fact the case according to Gaffney et al. (2006). Fortunately, the MCZ-collected specimens consist of skulls and shells from the same quarry (Gaffney and Wood, 2002). The large size, broad snout, and straight labial ridge (in anterior view) are characteristic of this species.

*Bairdemys winklerae* Gaffney et al., 2008

TYPE SPECIMEN: AMU-CURS 98 (Gaffney et al., 2008).

TYPE LOCALITY: North of El Picache, Urumaco Formation, state of Falcón, Venezuela.

HORIZON: Late Miocene, Urumaco Formation.

DIAGNOSIS: A species of *Bairdemys* differing from all other *Bairdemys* species in having an elongate, narrow snout with the labial ridge concave in ventral view, and a wide basisphenoid-quadrate contact; also differs from *B. hartsteini* in having a larger skull and no premaxillary notch; also differs from *B. venezuelensis* in having a narrower skull, a wider posterior triturating surface, no premaxillary notch, and a longer midline pterygoid contact; also differs from *B. sanchezi* in having a larger skull, a larger, anteriorly wider, basisphenoid, and a less extensive temporal and cheek emargination.

REFERRED MATERIAL: Probably AMU-CURS 96, AMU-CURS 97, and AMU-CURS 99, belong to this species, as these specimens have elongate snouts. The specimens come from the same stratigraphic level (quarry level) at the El Picache locality (11°14′ 40″N, 70°14′″4″E; top of the upper member in the Urumaco Formation). This locality represents the eastern equivalent of the "capa de Tortuga" located in Corralito (also top of the upper member).

PREVIOUS WORK: Sánchez-Villagra and Winkler (2006).

DISCUSSION: This species is described and figured in Sánchez-Villagra and Winkler (2006) and Gaffney et al. (2008). Its large size, elongate snout, and concave labial ridges are characteristic.

*Bairdemys sanchezi* Gaffney et al., 2008

TYPE SPECIMEN: Skull, jaws, and anterior plastral fragment (Gaffney et al., 2008). AMU-CURS 186; collector: Orangel Aguilera, Alcaldía del Municipio Urumaco, Colección Rodolfo Sánchez.

TYPE LOCALITY: Tío Gregorio, Falcón State, Venezuela (Aguilera, 2004). Locality coordinates: 11°14′43″N, 70°18′19″W. The Tío Gregorio locality represents the top of the upper member in the Urumaco Formation, and may be on the same stratigraphic level as the MCZ quarry in Tío Gregorio.

HORIZON: Upper Member of the Urumaco Formation.

DIAGNOSIS: A species of *Bairdemys* differing from all other *Bairdemys* species in having a low triturating surface convexity and shallow triturating surface concavity, a smaller basisphenoid acutely pointed anteriorly, a small skull, and an extensive cheek and temporal emargination; also differs from *B. hartsteini* in having a convex rather than straight labial ridge in ventral view; also differs from *B. venezuelensis* in having a long midline pterygoid contact and a premaxillary notch, and also differs from *B. winklerae* in having a short, broad snout with a convex

labial ridge in ventral view, a premaxillary notch, and a triturating surface that is narrower anteriorly and wider posteriorly.

REFERRED MATERIAL: None.

PREVIOUS WORK: Gaffney et al. (2008).

DISCUSSION: This specimen is described and figured in Gaffney et al. (2008). The small size, flatter triturating surface, and extensive temporal and cheek emargination provide ready distinction of this species from the other species of *Bairdemys*. The shell fragment consists of the entoplastron and most of both epiplastra. The scale pattern is very similar to that of *Bairdemys venezuelensis* figured in Gaffney et al. (2006: fig. 275).

*Bairdemys,* species indeterminate

SPECIMEN: AMNH 30000, a poorly preserved skull and partial carapace (Gaffney et al., 2008).

LOCALITY AND HORIZON: Castillo Formation, Venezuela; see Sánchez-Villagra et al. (2000), Sánchez-Villagra and Winkler (2006).

DISCUSSION: This skull has been figured in Sánchez-Villagra et al. (2000), Sánchez-Villagra and Winkler (2006), and discussed in Sánchez-Villagra and Scheyer (2010). Sánchez-Villagra and Winkler (2006) have most recently argued that it is a distinct species within *Bairdemys*. We agree, but a skull without sutures that is as poorly preserved as AMNH 30000 should not be named. It can be differentiated from the other four species recognized here by the posterior position of the condylus articularis, slightly wider anterior portion of the triturating surfaces, and the more horizontal orientation of the orbits.

Infratribe Stereogenyita, new

DIAGNOSIS: Members of the Subtribe Stereogenyina; labial ridge low and blunt; pinched snout (not known for *Brontochelys*); cheek emargination does not reach level of orbit; eustachian tube separated by bone from rest of fenestra postotica (not in *Cordichelys*); angle of front of skull exceeds 90° in contrast to the Infratribe Bairdemydita, in which it is 90° or less.

INCLUDED TAXA: *Shweboemys* Swinton, 1939; *Stereogenys* Andrews, 1901; *Brontochelys,* n. gen.; *Lemurchelys,* n. gen.

DISCUSSION: The low and blunt labial ridge is unique to this group among podocnemidids. The absence of cheek emargination, however, is found throughout the Infrafamily Erymnochelyodda and is known only for one specimen of *Stereogenys* among the Infratribe Bairdemydita.

***Brontochelys,*** new genus

TYPE SPECIES: *Shweboemys gaffneyi* Wood, 1970.

INCLUDED SPECIES: *Brontochelys gaffneyi.*

DIAGNOSIS: A podocnemidid of the Tribe Stereogenyini known from the skull; uniquely possessing large orbits that face forward to a greater degree than in other Tribe Stereogenyini and frontal that forms more of the dorsal orbital margin than in other Tribe Stereogenyini; medial edges of palatal cleft curved in contrast to the other Infratribe Stereogenyita (*Lemurchelys, Shweboemys* and *Stereogenys*); triturating surfaces relatively flat as in *Shweboemys* and in contrast to most Tribe Stereogenyini; jugal-pterygoid contact prevents palatine-parietal contact; basisphenoid very wide, wider than basioccipital, in contrast to most other Tribe Stereogenyini in which it is narrower.

DISTRIBUTION: Pakistan, Early Miocene.

ETYMOLOGY: From *Bronte*, Greek "thunder"; *chelys*, Greek "turtle," in allusion to the large size of the skull.

***Brontochelys gaffneyi***
(Wood, 1970), new combination

*Shweboemys gaffneyi* Wood, 1970

TYPE SPECIMEN: BMNH R.8570 (figs. 62–66), a nearly complete skull, lacking some of the preorbital area, most of the lateral and posterior skull roof, and most of the quadrates. Also figured and described in Wood (1970: figs. 1, 2; pls. 2B, 3B, 4B).

TYPE LOCALITY AND HORIZON: Unknown, but Wood (1970, q.v. for discussion) concluded that the type specimen was from Early Miocene sediments in or near the Bugti Hills, Baluchistan, Pakistan.

DIAGNOSIS: Genus is monotypic.

PREVIOUS WORK: Wood (1970).

DISCUSSION: The distinction of this genus relies on the unique anteriorly facing orbits and large frontal bone, as well as other palatal features not occurring in the infratribe Stereogenyita.

***Lemurchelys,*** new genus

TYPE SPECIES: *Lemurchelys diasphax,* new species.

INCLUDED SPECIES: *Lemurchelys diasphax,* new species.

DIAGNOSIS: A podocnemidid of the Tribe Stereogenyini known only from the skull; uniquely possessing a very deep crista supraoccipitalis base and adjoining parietal, deeper than in any other Tribe Stereogenyini, and the combination of a parallel-sided palatal cleft and broadly meeting pterygoids due to a short basisphenoid; snout shape wide as in *Stereogenys* and *Shweboemys* not narrow as in *Latentemys* and *Cordichelys*; ventral edge of orbital rim a curved surface not an acute edge as in all other Tribe Stereogenyini except *Brontochelys*; palatal concavity and convexity very low in contrast to *Bairdemys*; frontal and prefrontal flat in profile in contrast to *Bairdemys*; septum orbitotemporale with large postorbital and small palatine and parietal-palatine contact in contrast to *Shweboemys* and *Stereogenys*; base of crista supraoccipitalis and adjoining parietal very deep, deeper than in any other Tribe Stereogenyini.

DISTRIBUTION: Miocene of Egypt.

ETYMOLOGY: In allusion to its discovery in the Duke Primate Center, surrounded by a collection of live lemurs, many of which took a prolonged interest in our work.

***Lemurchelys diasphax,*** n. gen. et sp.

TYPE SPECIMEN: DPC 6425 (figs. 67–70), a nearly complete skull lacking the left otic region, the temporal roof covering, and the cheeks; DPC field number 86-1226.

TYPE LOCALITY: MG-L-16, Moghara, Egypt.

HORIZON: Moghara Fm., early Miocene (18–17 Ma; Miller, 1999).

DIAGNOSIS: As for genus.

ETYMOLOGY: Greek *diasphax,* meaning "cleft" in allusion to the cleft in the secondary palate characteristic of this group.

PREVIOUS WORK: None.

DISCUSSION: The distinction of this skull-based genus relies on the deep crista supraoccipitalis and the unique combination of palatal characters.

*Shweboemys* Swinton, 1939

TYPE SPECIES: *Shweboemys pilgrimi* Swinton, 1939: 548.

INCLUDED SPECIES: *Shweboemys pilgrimi* Swinton, 1939.

DIAGNOSIS: A podocnemidid of the Tribe Stereogenyini known from the skull; uniquely possessing an elongate basisphenoid that has very little palatine contact and very narrowly separates the pterygoids, which are almost in contact, in contrast to the longer basisphenoid, which broadly contacts the palatines in *Stereogenys*; pinched snout in contrast to Infratribe Bairdemydita; medial edges of palatal cleft parallel in contrast to the Infratribe Bairdemydita; basioccipital shorter than in all other Tribe Stereogenyini except *Stereogenys*; palatine with dorsal process in septum orbitotemporale that contacts parietal as in *Stereogenys* and in contrast to all other Tribe Stereogenyini.

DISTRIBUTION: Burma, Pliocene or Pleistocene.

DISCUSSION: This genus was erected by Swinton in 1939 on the basis of a single skull from Burma. Swinton recognized that it was a "pelomedusid" sensu lato and compared it with *Podocnemis* and *Stereogenys*. He was the first to determine the unique nature of the palatal cleft and recognize that this unique cleft also occurred in *Stereogenys*.

Wood in 1970 identified a second skull of *Shweboemys pilgrimi* (BMNH R.8432) using Swinton's description and new photographs of the type specimen from the Geological Survey of India. Wood (1970) also moved Andrew's "*Podocnemis*" *antiqua* to *Shweboemys* on the basis of the secondary palate and described a new species of *Shweboemys*, *S. gaffneyi*. At that point, the genus (essentially equal to our tribe Stereogenyini) consisted of three species: *pilgrimi*, *antiqua*, and *gaffneyi*.

In 1977, Jain described a new species of Pelomedusoides, *pisdurensis*, from the Late Cretaceous of India, first (Jain, 1977) assigning it to "*Carteremys*" then to *Shweboemys* (Jain, 1986). The change in generic assignment by Jain was prompted by the suggestion of one of us (E.S.G.) based on the published figures in Jain (1977). We still have not had an opportunity to examine the specimens, but, again based solely on the published figures, *pisdurensis* does not belong in *Shweboemys* and probably does not belong in the Tribe Stereogenyini. The figures of the ventral surface of the skull (supplemented by other photographs sent to E.S.G. by Jain) do show a broad palate but one that lacks the distinctive cleft that we argue is diagnostic for this group. From the photographs it is also difficult to be sure that the skull has the cavum pterygoidei diagnostic of the Podocnemididae. Therefore, we provisionally exclude *pisdurensis* from *Shweboemys* and the Tribe Stereogenyini and place it incertae sedis without generic assignment, within the Pelomedusoides, pending further study.

In the present study we remove *Shweboemys gaffneyi* Wood to a new genus, *Brontochelys*. We also remove *Shweboemys* (*Podocnemis*) *antiqua* (Andrews) to another new genus, *Cordichelys*. As we currently recognize *Shweboemys* it consists only of the type species, *Shweboemys pilgrimi* Swinton. The increase in taxonomic diversity in the podocnemidids with a secondary palate developed in this paper is consistent with current practice in Recent turtles, particularly Pelomedusoides.

### *Shweboemys pilgrimi* Swinton, 1939

TYPE SPECIMEN: Geological Survey of India number 17255, a partial skull consisting of the anterior portion with palate, lacking otic chambers and posterior and lateral areas of skull roof (not seen by present authors). Figured in Swinton (1939: figs. 1, 2) and Wood (1970: pl. 1).

TYPE LOCALITY: "One mile NNE of Mauktet, Shwebo District, Burma" (Wood, 1970: 9).

TYPE HORIZON: Irrawaddy Beds, Pliocene or Pleistocene, fide discussion in Wood (1970), but a Miocene age cannot now be excluded.

DIAGNOSIS: Genus is monotypic.

REFERRED SPECIMEN: BMNH R.8432, a partial skull (figs. 71–74) consisting of the anterior portion with palate, lacking right otic chamber, some of left otic chamber, and lateral and posterior skull roof. Figured and described in Wood (1970: pls. I, II, III; 2A, 3A, 4A). Only data is "Burma" (Wood, 1970).

PREVIOUS WORK: Swinton (1939), Wood (1970).

### *Stereogenys* Andrews, 1901

TYPE SPECIES: *Stereogenys cromeri* Andrews, 1901.

INCLUDED SPECIES: At the present time, we are including only the skull-based *Stereogenys cromeri* in the genus. We realize that a number of other taxa have been named as species of *Stereogenys* that are shell based. These species are listed below, but we do not know what generic allocation would be likely for them.

DIAGNOSIS: A podocnemidid of the Tribe Stereogenyini known from the skull; uniquely possessing a secondary palate longer than in any other Tribe Stereogenyini, having a triturating surface of premaxilla with accessory ridge medial to labial ridge, and a basisphenoid that widely contacts the palatines and widely separates the pterygoids; pinched snout in contrast to Infratribe Bairdemydita; medial edges of palatal cleft parallel in contrast to the Infratribe Bairdemydita; basioccipital shortest of all Tribe Stereogenyini; palatine with large dorsal process in septum orbitotemporale that contacts parietal as in *Shweboemys* in contrast to all other Tribe Stereogenyini; triturating surface of premaxilla with accessory ridge medial to labial ridge in contrast to all other Stereogenyini.

DISTRIBUTION: Late Eocene, Egypt.

DISCUSSION: Andrews (1906: 298) assigned shells to *Stereogenys* by the following reasoning:

> Although in no case have the carapace and plastron been found associated with the skull in such a manner as to leave no doubt that they belong to the same individual, nevertheless the shell now to be described may be regarded with reasonable certainty as belonging to the present species. In the first place, this form of shell, like

the skull, is the commonest occurring in the Qasr el-Sagha beds, and in the second place it differs widely from the shell of *Podocnemis*, the only other Pleurodiran genus found in this horizon.

Commonality of occurrence can be used to associate skulls and shells in turtles only when there are a large number of specimens. There are rarely enough specimens (and that is certainly the case here) to make a statistical argument, and there are too many exceptions known. The "*Podocnemis*" referred to above was *P. antiqua*, here considered as *Cordichelys antiqua,* another tribe Stereogenyini member, closely related to *Stereogenys*, so that part of the argument is also problematic. To date there have been no skull-shell associations for *Stereogenys.* The shell-based species "*Stereogenys*" *libyca* Andrews, 1903, and *"Stereogenys" podocnemoides* Reinach, 1903b, are not assignable to genus on the basis of the shell, and they do not have skull material associated with them.

Nonetheless, the shells claimed by Andrews (1903: 119) to belong to the skull-based taxon *Stereogenys cromeri,* do have a distinctive set of characters: carapace oval and depressed, seven neural bones, the first one pentagonal and not meeting the nuchal bone but separated from it by midline contact of first pair of costal bones, buttresses relatively small, intergular scale large, separating both gulars and humerals, gular and humeral scales entirely on epiplastra. These shells could in fact belong to *Stereogenys cromeri*, as this shell type has not yet been associated with any skull. Although we describe this shell taxon below, there is no evidence linking it with *Stereogenys*.

*Stereogenys cromeri* Andrews, 1901

TYPE SPECIMEN: CGM 10027, apparently now lost (C. Walker, personal commun., BMNH), nearly complete skull and jaws, partially crushed dorsoventrally, surface badly pitted and eroded. Figured in Andrews (1901: fig. 4) and Andrews (1906: fig. 95; pl. 25, figs. 2, 3). Represented by BMNH R.3007, a cast.

TYPE LOCALITY: "North of Birket el-Qurun," Andrews (1906: 296).

TYPE HORIZON: "Qasr el-Sagha beds (Middle Eocene)," Andrews (1906: 296); now regarded as Late Eocene (Holroyd et al., 1996; Seiffert, 2006; see also Moustafa, 1974, for general discussion and map).

DIAGNOSIS: Genus is monotypic.

REFERRED SPECIMENS: DPC 4120 (figs. 77, 78), locality 83-L-37, from the Dir Abu Lifa Member, Qasr el-Sagha Fm. (see Holroyd et al., 1996: fig. 1 for stratigraphic position), field number 83-1118, well-preserved skull, undistorted and completely free of matrix, lacking left otic chamber, skull roofing elements, and premaxillae.

All of following specimens have "Qasr el-Sagha, Fayum" as locality data, and it is likely that at least some came from the "bone beds" (Beadnell, 1901), as Beadnell explicitly noted the turtles in his report. These "bone beds" are now recognized as part of the Dir Abu Lifa Member (Holroyd et al., 1996). CGM 10031, cast is BMNH R.8442, original presumed lost (C. Walker, personal commun., BMNH), partial skull crushed dorsoventrally; BMNH R.3190, a partial skull Andrews (1906: fig. 95), has most complete cheek of *Stereogenys* specimens, showing that there was not an extensive emargination; BMNH R.3189, laterally crushed skull lacking roofing elements, Andrews (1906: pl. 25, fig. 1), completely closed palate is an artifact of crushing, and sutures that are so convincingly shown are drawn in ink, a number of them incorrectly; BMNH R.3191 (figs. 79, 80), a braincase and partial palate with endocast, identified as *Stereogenys* on basis of extent of secondary palate, and basisphenoid contacting palatines and separating pterygoids; BMNH R.3906, consists of a poorly preserved partial skull and lower jaws, the lower jaws are very similar to the type lower jaws, CGM 10027, skull, however, is from a much smaller individual and does not belong with the jaws, although the ventral surface is poorly preserved, the posterior margins of the secondary palate are present, and they are more posteriorly placed than in CGM 10027, so it may not even be *Stereogenys*.

A lower jaw, University of Michigan 161 (fig. 81), Wadi Hitan, Fayum, can possibly be attributed to this species, although it is not

associated with a skull and has some differences from the Andrews figured jaw (1906: pl. 25, fig. 3).

PREVIOUS WORK: Andrews (1901, 1906), Wood (1970).

## DUBIOUS TAXA

### Podocnemididae Incertae Sedis

These are taxa that are taxonomically valid and diagnosable, but lack enough characters to reasonably analyse within the Podocnemididae.

#### *Cambaremys* França and Langer, 2005

TYPE SPECIES: *Cambaremys langertoni* França and Langer, 2005.

DISTRIBUTION: Late Cretaceous, Brazil.

DIAGNOSIS: A medium-size Pelomedusoides pleurodire (230 mm straight carapace length) known only from the shell and associated postcranial elements differing from other South American Cretaceous and Early Tertiary Pelomedusoides in having vertebral scales 2–4 relatively wide and hexagonal, a relatively long narrow nuchal bone (also long and narrow in Peirópolis A), first neural four sided, axillary buttress not extending onto second costal but reaching second peripheral anteriorly, suture for axillary buttress broad and curving with parallel sides, bridge peripherals unguttered, iliac attachment area on seventh costal with concave anterior margin that crosses from the eighth onto the seventh costal both medially and laterally; internal gutter of posterior peripherals and pygal absent.

#### *Cambaremys langertoni* França and Langer, 2005

TYPE SPECIMEN: CPP 0252, partial carapace, mesoplastron, xiphiplastra, limb and vertebral elements (França and Langer, 2005).

TYPE LOCALITY: "Quarry 2 of Price (see Campos and Kellner, 1999), at 900 m high, in the Serra do Veadinho area, municipality of Uberaba, Minas Gerais, Brazil; about 2.5 km to the N-NW of the village of Peirópolis," 19°43′12″S, 47°45′12″W (França and Langer, 2005: 395). This locality is close to, but not the same as, the site of the large-scale excavations at Caiera Quarry, called "outcrop 1" in Carvalho et al. (2004: 978), Novas et al. (2008: 628), and shown in the quarry map in Kellner et al. (2005: 533), which have yielded the large collection of turtle specimens including Peirópolis A, Peirópolis B, and the types of *Pricemys* and *Peiropemys*. Novas et al. (2008: fig. 2) show a map with "outcrop 1" and "outcrop 2" which are presumed to be these two localities. Apparently (ibid.) the stratigraphic levels of the two sites are about the same, and we presume that *Cambaremys, Pricemys,* and *Peiropemys* were contemporaneous with each other and with the shell taxa Peirópolis A and Peirópolis B.

HORIZON: Serra da Galga Member, Marília Fm., Late Cretaceous, probably Maastrichtian (França and Langer, 2005: 395).

DIAGNOSIS: As for genus.

REFERRED MATERIAL: Known only from the type. We know of no additional specimens that could be referred to this taxon.

PREVIOUS WORK: França and Langer (2005, 2006), Oliveira and Romano (2007), Romano et al. (2009).

DISCUSSION: Our understanding of this taxon is based on the type description (França and Langer, 2005), as well as the dissertation in which the type (CPP-0252) is described in detail (França, 2004). We agree with Broin (1991) and França and Langer (2006) that there are multiple taxa represented in the material from late Cretaceous horizons in the vicinity of the town of Peirópolis. We have identified three shell morphologies: *Cambaremys* (França and Langer, 2005), Peirópolis A, Peirópolis B, and two types of skulls, *Pricemys caiera* and *Peiropemys mezzalirai.* To our knowledge, there are no skull-shell associations for the Peirópolis material (see also Broin, 1991), so at this time we name only the skulls with the understanding that if and when skull-shell associations are found, the nomenclature may need to be revised.

Romano et al. (2009) have suggested that the incompletely known *Cambaremys langertoni* is probably a juvenile *Roxochelys wanderleyi.* We disagree with this assessment. We have studied the type of *Roxochelys wanderleyi,* which is a plastron and partial carapace, and our independent assessment agrees with

Romano et al. (2009: figs. 2B, 3C) that two additional complete shells (DGM LE 307, DGM Mezzalira) can be assigned to *Roxochelys wanderleyi* (see discussion in Systematics). This additional material allows a relatively complete understanding of the shell of this taxon. Although the type and only known specimen of *Cambaremys langertoni* is a carapace with only a small portion of the plastron, it is clear that these taxa differ in several significant features (table 4). The nuchal of *Cambaremys* is longer than wide while that of *Roxochelys* is the widest relative to length among the Cretaceous and early Tertiary South American podocnemidids we have studied (fig. 94). Furthermore, the nuchal of *Cambaremys* is narrower anteriorly than in *Roxochelys,* which is the widest in this set of taxa. It addition, the axillary buttress scar is parallel sided in *Cambaremys* as is shown for Peirópolis A (fig. 93A) and not tapering laterally as in *Roxochelys* (and Peirópolis B, fig. 93B), and the second costal is not thickened posterior to the axillary buttress in *Cambaremys* as it is in *Roxochelys*. Therefore, we conclude that although *Cambaremys* is poorly known and incertae sedis, it is not *Roxochelys.* In some ways it is more similar to Peirópolis A, but we have refrained from referring Peirópolis A to *Cambaremys* because the type of *Cambaremys* lacks important autapomophic features of Peirópolis A (see table 4 and below).

França and Langer (2005: 408–409) discuss and reject the possibility that *Cambaremys* is a juvenile "*Podocnemis*" *brasiliensis.* But Oliveira and Romano (2007) and we consider the latter taxon to be a nomen dubium.

### *Cerrejonemys* Cadena, Bloch, and Jaramillo, 2010

TYPE SPECIES: *Cerrejonemys wayuunaiki* Cadena, Bloch, and Jaramillo, 2010.

DISTRIBUTION: Paleocene of northern Colombia.

ETYMOLOGY: See Cadena et al. (2010).

DIAGNOSIS: As for species.

### *Cerrejonemys wayuunaiki* Cadena, Bloch, and Jaramillo, 2010

TYPE SPECIMEN: "University of Florida, Florida Museum of Natural History Vertebrate Paleontology Collections, Gainesville, Florida/Museo Geológico, at the Instituto Nacional de Investigaciones en Geosciences, Minería y Quimica, Bogotá, Colombia" UF/IGM 33, Cadena et al. (2010: 368). The presence of the holotype and only known specimen in two widely separated institutions is unexplained in Cadena et al. (2010).

TYPE LOCALITY: Cerrejón Coal Mine, Guajira Peninsula, Colombia. See Cadena et al. (2010) for further information.

HORIZON: Cerrejón Fm., mid to late Paleocene, see Cadena et al. (2010) for further information.

DIAGNOSIS: Cadena et al. (2010: 369). We do not dispute the conclusion that this taxon is diagnosable and separate from previously known taxa.

ETYMOLOGY: See Cadena et al. (2010).

REFERRED MATERIAL: None.

PREVIOUS WORK: Cadena et al. (2010).

DISCUSSION: Cadena et al. (2010) produce a character matrix and phylogenetic analysis concluding that *Cerrejonemys* is the sister taxon to the genus *Podocnemis.* The principal character supporting this resolution is the relatively small postorbital and the jugal-parietal contact in *Cerrejonemys.* This may prove to be the case, but in our admittedly limited examination of the specimen, which is badly crushed, these sutures seem ambiguous, as they are in the published photographs. *Cerrejonemys* has a cavum pterygoidei, so it is a podocnemidid, but it apparently lacks the *Podocnemis*-like triturating surface ridges, and the temporal emargination is more extensive, comparable to that seen in *Lapparentemys* rather than *Podocnemis.* So, until better material is available, we feel that *Cerrejonemys* is best considered Podocnemididae incertae sedis.

### *Kenyemys* Wood, 1983

TYPE SPECIES: *Kenyemys williamsi* Wood, 1983.

DISTRIBUTION: Pliocene of Kenya.

DIAGNOSIS: From Wood (1983: 74):

> Differing from all other members of the family by the following combination of characters: (1) a series of elongate tuberosities forming an interrupted keel extending along the midline rearward from the dorsal surface of the second

TABLE 4
**Comparison of Shells of Six South American Late Cretaceous and Early Tertiary Podocnemidid Turtles**

| | *Bauruemys elegans* | *Cambaremys* | Peiropolis A | Peiropolis B | *Lapparentemys vilavilensis* | *Roxochelys wanderlyi* |
|---|---|---|---|---|---|---|
| Overall size of carapace | small, about 125 mm | medium, about 230 mm | large, about 700 mm | small, about 125 mm | medium, about 400 mm | Medium, about 300 mm |
| Shell texture of concentric rings | present | absent | absent | present, but weak | absent, but variable | absent |
| Nuchal shape | short and wide | long and narrow | long and narrow | short and wide | short and wide | short and wide |
| Second neural four sided | always | no, but only known from type | four sided in one specimen, six sided in two | first costals suggest six sided | six sided | six sided |
| Bridge peripherals guttered dorsally | yes | no | yes | no | yes | no |
| Anterior limit of axillary buttress | peripheral 3 | peripheral 2 | peripheral 3 | not known | peripheral 3 | peripheral 3 |
| Suture for axillary buttress of hyoplastron narrows anterolaterally | yes | no | no | yes | no | yes |
| Second costals thickened at suture to first costal | yes | no | no | yes | no | yes |
| Inguinal buttress suture on fifth costal | broader and more lateral | broader and more lateral | broader and more lateral | narrower and extending further medially | broader and more lateral | narrower and extending further medially |
| Iliac scars on seventh costals with concave anterior margin | no | yes | no | not known | yes | yes |
| Internal gutter on posterior peripherals 10, 11 and pygal | no | no on peripheral 11, pygal not known | yes | no | no | no |
| Epiplastron shape | slightly thickened lip with a single large posterio-medial process | not known | thickened, rounded lip without single large posterior-medial process | slightly thickened with a single large posterior-medial process | thickened, rounded lip without single large posterior-medial process | slightly thickened lip with a single large posterior-medial process |
| Intergular width | narrow | not known | narrow | not known | narrow | wide |
| Gular reaches epiplastral suture | varies, but usually yes | not known | no | not known | yes | no |
| Humeral contact on midline | short | not known | long | not known | short | long |
| Pectoral scutes reach epiplastron | yes | not known | no | not known | yes | no |
| Pectoral scutes reach entoplastron | yes | not known | yes | not known | yes | yes |
| Pectoral scutes reach mesoplastron | no | no | yes | not known | varies | no |

neural bone; (2) six neural bones forming a continuous series, the anterior end of the first abutting directly against the rear margin of the nuchal bone and the sixth one being heptagonal; (3) outer corners of nuchal bone extending beyond lateral margins of first vertebral scute; (4) pentagonal shape of first vertebral scute; (5) only eighth and posterior part of seventh pairs of pleural bones [costal bones in our nomenclature] meeting at midline of carapace; (6) anterior plastral lobe truncated; (7) triangular intergular scute not overlapping anterior end of entoplastron and only partially separating the gular scutes along the midline axis of the plastron.

DISCUSSION: The best statement about the relationships of yet another shell-only species is "The relationship of *Kenyemys* to other African pelomedusids [= Pelomedusoides] is at present obscure" (Wood, 1983: 79).

*Kenyemys williamsi* Wood, 1983

TYPE SPECIMEN: National Museum of Kenya NMK LT 127, a nearly complete but somewhat crushed, shell, figured in Wood (1983: figs. 1–5).

TYPE LOCALITY: Lothagam Hill, southwest Turkana District, Kenya (Wood, 1983).

HORIZON: Lothagam 1, Pliocene (Wood, 1983: 79).

Peirópolis A, unnamed shell taxon

SYNONYMY: It is likely that this shell-based form is the same taxon as one of the two skulls named from this locality, *Pricemys* or *Peiropemys*. Due to the disassociated nature of the DGM collections from Peirópolis (see below), it is not possible to assign this postcranial material to one of these two new skull-based taxa or to recognize other taxa based on postcrania that may be present. The shell material of Peirópolis A is larger in size than the postcranials of Peirópolis B, and the skull of *Pricemys* is larger than the skull of *Peiropemys,* consistent with the speculation that Peirópolis A is the shell of *Pricemys.* However, it should be kept in mind that at least one other shell taxon, *Cambaremys langertoni,* although distinctly smaller than Peirópolis A, is present at a locality close to and at the same level as the Caiera Quarry (see discussions under *Cambaremys* and *Peiropemys*).

DISTRIBUTION: Caiera Quarry, near village of Peirópolis, near city of Uberaba, Minas Gerais State, Brazil (see França and Langer, 2005, for map). Collected from the quarry at base of the same hill (locality 1) near the lime plant that yielded the material referred to Peirópolis B, below, and the type skulls of *Pricemys caiera* and *Peiropemys mezzalirai.* See locality discussion under *Peiropemys* for more information.

HORIZON: Serra da Galga Member, Marília Fm. (see Candeiro, 2009, and references).

REFERRED SPECIMENS: Unnumbered complete carapace and plastron on top of DNPM/DGM cabinets and a DGM specimen labeled "Peirópolis 321." Other disarticulated and uncataloged material shows autapomorphies of these two specimens and probably represent the same taxon.

(1) Peirópolis 321, a complete plastron, at least some carapace and some cervical parts, all disarticulated. The plastron of 321 is in a drawer labeled: "Desmonte 1967 Peirópolis Mun. Uberaba."
(2) MCT 1499-R, a large shell from Peirópolis. Most of the carapace, the plastron, pelvis, and first thoracic are present. It is prepared with the plastron side up; some of anterior lobe is separate. It is labeled Peirópolis, Caiera, locality #1.
(3) DNPM uncataloged, shell from Peirópolis collected by Langerton, has a thickened dorsal lip of the epiplastra, which appears to be characteristic of Peirópolis A.

DIAGNOSIS: This large pelomedusoides pleurodire (to 700 mm straight carapace length) differs from other South American Cretaceous and early Tertiary Pelomedusoides in having no distinct surface sculpture; vertebral scales 2–4 relatively wide and hexagonal; nuchal bone relatively long and narrow; first or second neural four sided; axillary buttress not extending onto second costal and reaching to third peripheral anteriorly; suture for axillary buttress broad and curving with parallel sides; second costal not thickened to support axillary buttress; bridge peripherals guttered dorsally; iliac attachment area on seventh costal with convex anterior margin; costal 8 wide, contacting peripherals 9, 10, and 11; costal 7 narrow allowing peripheral 9 to contact

costals 6, 7, and 8; internal gutter of posterior peripherals and pygal strongly developed.

Plastron with epiplastron having thickened anterior edge with rounded lip, and lacking single, large posteromedial process; xiphiplastron with C-shaped anal notch (except in MCT 322-R); gular scales restricted to epiplastra; intergular scale narrow; long humeral scale contact on midline; pectoral scales contact entoplastron and mesoplastra but not epiplastra.

PREVIOUS WORK: Mentioned in Broin (1991).

DISCUSSION: Based on its large size, one could associate this material with the large skull of *Pricemys.*

Peirópolis B, unnamed shell taxon

SYNONYMY: It is possible that this shell-based form is the same taxon as one of the two skulls named from this locality, *Pricemys* or *Peiropemys*. Due to the disassociated nature of the DGM collections from Caiera Quarry, Peirópolis (see below), it is not possible to assign this postcranial material to one of these two new skull-based taxa. But if one wishes to speculate, the shell material of Peirópolis B is smaller in size than the shell of Peirópolis A, and the skull of *Peiropemys* is smaller than the skull of *Pricemys,* consistent with the speculation that Peirópolis B is the shell of *Peiropemys.* The other Peirópolis area shell taxon (but not from Caiera Quarry), *Cambaremys langertoni,* is also distinctly smaller than Peirópolis A, and could be interpreted as another contender for the shell of *Peiropemys.*

DISTRIBUTION: Locality #1, Caiera Quarry, near village of Peirópolis, same quarry as Peirópolis A, *Pricemys caiera,* and *Peiropemys mezzalirai.* See locality discussion under *Peiropemys* for more information.

HORIZON: Serra da Galga Member, Marília Fm. (see Candeiro, 2009, and references).

REFERRED SPECIMENS: Peirópolis B is the smallest of the three shell taxa from this locality and the one for which there is the most limited amount of material. The material is all disarticulated but some of it is associated. At present we have the nuchal, costals 1, 5, 7, and 8, peripherals 1, 8 to 11, the suprapygal, and the pygal. We can only speculatively assign plastron material to this taxon on the basis of size.

DIAGNOSIS: Shell relatively small (about 125 mm straight carapace length); shell texture with weak concentric rings, as in *Bauruemys elegans*; nuchal bone relatively short and wide; second neural bone may have been six sided; bridge peripherals smooth, not guttered; axillary buttress attachment area on first costal narrows anterolaterally; first costal–second costal contact area not uniform, thickened near axillary attachment scar; inguinal buttress attachment area on fifth costal relatively narrow and more extensive medially in contrast to Peirópolis A; iliac attachment area on seventh costal with concave anterior margin; ventral surface of peripheral 11 and pygal without gutter or ventral flange.

Possible plastral elements have epiplastron without the thickened anterior margin seen in Peirópolis A, and with a single, large posteromedial process; xiphiplastron with V-shaped anal notch.

PREVIOUS WORK: Mentioned in Broin (1991).

DISCUSSION: Based on characters in common, Peirópolis B could be identified as *Bauruemys.* However, the speculative association of plastral and some of the carapacial elements with the only associated material, DNPM MCT uncataloged (consisting of nuchal, costals 1, 5, 7, 8, peripherals 1, 8–11, suprapygal, pygal), is based solely on size. Furthermore, there is the definite possibility that at least some of this material belongs to the skull taxon, *Peiropemys*, which differs significantly from *Bauruemys.* We are also aware of the strongly conservative nature of pelomedusoides shells, which typically have easily differentiated skulls and very similar shells. So we refrain from identifying this as an unnamed species of *Bauruemys,* or as the skull of *Peiropemys.*

We should emphasize again that the individually disarticulated bones that we identify as Peirópolis A and Peirópolis B are, with a few stated exceptions, not associated with other elements. We informally associate them here on the basis of size, differences from *Cambaremys*, and in the case of some Peirópolis A material, with morphology of an articulated shell. It is possible that there are more than three species in these collections. Our speculative association of the

smaller Peirópolis B shell elements with the smaller skull of *Peiropemys* and the larger Peirópolis A shell elements with the larger skull of *Pricemys* is based only on size. All of these assumptions are weak at best, and that is why we have not formalized or used them in the phylogenetic analysis.

### *"Podocnemis" argentinensis* Cattoi and Freiburg, 1958

TYPE SPECIMEN: MACN 17.988, partial plastron lacking anterior and posterior portions, figured by Cattoi and Freiburg (1958: fig. 1 and unnumbered plate).

TYPE LOCALITY AND HORIZON: "Parte media de las 'Margas Multicolores,' Quebrada Queñoal, en el flanco occidental del espolón Esquina Blanca, Q. de Humahuaca, Provincia de Jujuy, Argentina" (Cattoi and Freiburg, 1958: 60).

DIAGNOSIS: See Cattoi and Freiburg (1958: 60, 61) for diagnosis, but we have been unable to find any characters in it that differentiate this species from most species of podocnemidids. The most variable, although not necessarily most informative, parts of the podocnemidid plastron are the anterior plastral lobe with its intergular-gular-humeral scale arrangements and the posterior anal notch and xiphiplastral eminences. These areas are unfortunately missing in the type specimen of "*Podocnemis*" *argentinensis* Cattoi and Freiburg (1958: fig. 1 and unnumbered plate). A left epiplastron (Cattoi and Freiburg, 1958: unnumbered plate, lower), MACN 16.553, does show a small gular scale completely separated on the midline and a humeral scale partially separated on the midline. However, none of these features serve to distinguish this species.

REFERRED MATERIAL: Specimens in AMNH, see below.

PREVIOUS WORK: Cattoi and Freiburg (1958); Cattoi and Freiburg (1961, which is an abstract announcing new specimens with no taxonomic novelties), Broin (1991: 515).

DISCUSSION: The reality of this species is actually established by material in the AMNH from Jujuy Province, Argentina, presumed to come from or near the type locality of "*Podocnemis*" *argentinensis* (label), which includes more than a dozen partial shells and a nearly complete skull and jaws. The skull, now under study by Marcelo de la Fuente (Museo de La Plata) shows a complete cavum pterygoidei with a relatively short skull and wide triturating surfaces bearing accessory ridges. This skull may allow *argentinensis* to be substantiated and objectively diagnosed. A brief description of this material can also be found in Broin (1991: 515).

### *"Podocnemis" geologorum* Simpson, 1943

TYPE SPECIMEN: Originally AMNH 6781 but sent to Venezuela (Museo de Ciencias Naturales, Caracas; catalog number not known) before 1965, right posterior portion of carapace and plastron figured by Simpson (1943: figs. 1, 2).

TYPE LOCALITY AND HORIZON: "Serie de Zaraza, Mioceno. Pozo Rendivú, en la Quebrada Honda, cerca de Zaraza, Estado Guárico, Venezuela" (Simpson, 1943: 56). Sánchez-Villagra and Scheyer (2010: 184) gave more information on the age of the unit, as "late Early–early Middle Miocene."

DIAGNOSIS: See Simpson (1943: 56). The diagnosis is not very comparative and mentions only *Podocnemis expansa*. The figures show a pygal notch, which, if actually present (the specimen is not well preserved in this area and there are no photographs published), would be unique among podocnemidids. The anal notch is narrow, but this is not unique.

REFERRED MATERIAL: None.

PREVIOUS WORK: Wood and Díaz de Gamero (1971) mentioned this taxon in passing, suggesting that it is so poorly preserved that it could even be a chelid, but that it was not *Podocnemis*, based on the pygal shape. Sánchez-Villagra and Scheyer (2010) gave a new figure of the shell (ibid.: fig. 9.3), but were unable to confirm the presence of mesoplastra.

DISCUSSION: The inadequacy of the material prevents a comparative diagnosis and phylogenetic analysis.

### *"Podocnemis" medemi* Wood, 1997

TYPE SPECIMEN: IGM 1863, plastron and partial carapace, figured by Wood (1997: figs. 9.3, 9.4B).

TYPE LOCALITY: Cuenca de Melgar, Carmen de Apicalá, upper Magdalena River valley, Columbia (see Kay, et al., 1997, for locality data and references).

HORIZON: Honda Group (Wood, 1997).

DIAGNOSIS: "Differs from all other pelomedusids referred to *Podocnemis* in having a relatively short, rounded anterior and posterior plastral lobes; extremely narrow, V-shaped anal notch; proportionately small, squarish first pair of marginal scutes; enormous size (estimated midline carapace length = 101.5 cm); and position and shape of ischial scar on xiphiplastron (triangular in shape, expanded laterally, and moderately withdrawn from margin of anal notch)" (Wood, 1997: 159).

REFERRED MATERIAL: See Wood (1997).

PREVIOUS WORK: Wood (1997).

DISCUSSION: Although this is another shell species readily differentiated from other shell species, its phylogenetic relationships are characterized by Wood (1997: 168) "The relationship of *Podocnemis medemi* to other members of the genus is unclear." As with a number of these incertae sedis species, the absence of a good shell character diagnosis for the living *Podocnemis* is a problem preventing identification of these taxa as *Podocnemis.*

### *"Podocnemis" negrii* Carvalho, Bocquentin, and Lapparent de Broin, 2002

TYPE SPECIMEN: UFAC-PV 4441, partial carapace and partial plastron figured by Carvalho et al. (2002: figs. 1, 2).

TYPE LOCALITY: Five km south of Rio Branco, Acre, Brazil (Carvalho et al., 2002).

HORIZON: Solimões Fm., Miocene (Carvalho et al., 2002).

DIAGNOSIS: Differs from other *Podocnemis* in having a midline crest formed in the area of the second and third vertebral scales, with an apex on the sulcus between the scales; lacks plastral tubercles; anterior plastral lobe is relatively long and the gular and intergular scales are relatively short; most similar to *Podocnemis sextuberculata* (Carvalho et al., 2002).

REFERRED MATERIAL: Only the holotype.

PREVIOUS WORK: Carvalho et al. (2002).

DISCUSSION: Although Carvalho et al. (2002) argue that this species is the sister taxon to *Podocnemis sextuberculata*, they do not produce diagnostic characters arguing that it belongs to the genus *Podocnemis.* Even though this shell is similar to *P. sextuberculata*, the characters in common are not unique among the family and do not securely identify the shell as a member of the genus *Podocnemis.* The fact that this is one of the oldest records for this genus is therefore in doubt. The oldest secure record for *Podocnemis* is *P. bassleri,* which may be a synonym for *P. expansa.*

### *"Podocnemis" pritchardi* Wood, 1997

TYPE SPECIMEN: UCMP 63782, shell, figured by Wood (1997: figs. 9.1, 9.4A).

TYPE LOCALITY: UCMP locality V4531, upper Magdalena River valley, Columbia (see Kay et al., 1997, for locality data and references).

HORIZON: La Victoria Fm., Miocene (see Kay et al., 1997, for geology).

DIAGNOSIS: "Differs from all other South American pelomedusids referred to *Podocnemis* in having very narrow, almost rectangular, laterally placed mesoplastra; outer surfaces of the bridges curving downward and outward; extreme dorsoventral flattening of the shell; only six rather than seven neural bones; ischial scar on xiphiplastron very narrow along its entire length and situated directly adjacent to anal notch" (Wood, 1997: 156).

REFERRED MATERIAL: See Wood (1997: 156).

PREVIOUS WORK: Wood (1997).

DISCUSSION: Some of the diagnostic features might be questioned: the "extreme" flattening may be due to postmortem crushing and laboratory reconstruction as the buttresses show signs of damage, and the number of neurals varies considerably at six vs. seven among other *Podocnemis* species. The remaining characters do distinguish this species. However, the absence of a good diagnosis for the living *Podocnemis* is a problem recognized by the author: "Although it is possible that all the pelomedusids [= Pelomedusoides] described here [*medemi*

and *pritchardi*] may eventually prove to be genuine representatives of *Podocnemis*, it is by no means certain at present" (Wood, 1997: 156).

*Roxochelys* Price, 1953

TYPE SPECIES: *Roxochelys wanderleyi* Price, 1953.

DISTRIBUTION: Late Cretaceous of Brazil.

DIAGNOSIS: Referral of MCT 1722-R and DGM uncataloged "Mezzalira" specimen (figured in Romano et al., 2009: figs. 2B, 3C; see also Mezzalira, 1959, 1966) to *R. wanderleyi* allow for an expanded diagnosis. This medium-size Pelomedusoides pleurodire (about 300 mm straight carapace length) differs from other South American Cretaceous and Early Tertiary Pelomedusoides in having fine surface sculpture consisting of small polygons; vertebral scales 2–4 relatively wide and hexagonal; a relatively short, wide nuchal bone that is wide anteriorly; first neural four sided; axillary buttress extending onto second costal and reaching to third peripheral anteriorly, suture for axillary buttress broad medially and narrow laterally, second costal thickened to support axillary buttress, bridge peripherals unguttered; iliac attachment area on seventh costal with concave anterior that crosses from the eighth onto the seventh costal both medially and laterally; internal gutter of posterior peripherals and pygal absent; gular scales restricted to epiplastra; intergular scale wide; long humeral contact on midline; pectoral scales contact entoplastron but not epiplastra or mesoplastra.

*Roxochelys wanderleyi* Price, 1953

TYPE SPECIMEN: MCT 216-R, a partial carapace and partial plastron. Not lost, contrary to Candeiro et al. (2006: 927) (G.R. Oliveira, personal commun.).

TYPE LOCALITY: Araçatuba, Jubia (municipality of Mirandópolis, São Paulo State, Brazil (Price, 1953; Candeiro et al., 2006).

HORIZON: Adamantina Fm., Turonian-Santonian (Candeiro et al., 2006).

DIAGNOSIS: As for genus.

REFERRED MATERIAL: MCT 1722-R; DGM uncataloged "Mezzalira" shell (figured in Romano et al., 2009: figs. 2B, 3C; Mezzalira, 1959: 5, 6, locality 14).

PREVIOUS WORK: Mezzalira (1959, 1966, 1981, 1989), Broin (1991), Oliveira and Romano (2007). Oliveira and Romano (2007) correctly considered this species a nomen dubium, but with the addition of complete shells to the hypodigm, we feel that the species has risen to the level of diagnosable but incertae sedis.

DISCUSSION: The name *Roxochelys wanderleyi* Price, 1953, was applied to DGM 216-R a partial carapace and partial plastron. We agree that a shell figured by Romano et al. (2009: figs. 2B, 3C), collected by the geologist S. Mezzalira (the "Mezzalira" shell), can be identified as *Roxochelys wanderleyi* (see below). Furthermore, after additional study of MCT 1722-R (LE 307) it is apparent that this specimen also should be referred to *Roxochelys wanderleyi.*

Broin (1991) suggests that *Roxochelys wanderleyi* be considered a junior synonym of *R. harrisi* on the basis of similar ornamentation. However, this suggestion has not been followed in the recent literature (França and Langer, 2006; Oliveira and Romano, 2007; but see Candeiro et al., 2006). We concur with Oliveira and Romano (2007) that both "*Podocnemis*" *harrisi* Pacheco, 1913, and "*Podocnemis*" *brasiliensis* Staesche, 1937, should be considered nomina dubia.

*"Stereogenys" libyca* Andrews, 1903

TYPE SPECIMEN: BMNH R.3039, a carapace and plastron lacking part of the left side. This specimen was returned to the CGM in the 1960s, but the authors have been unable to locate it or determine its CGM number, so we use the original BMNH number.

TYPE LOCALITY: North of Lake Qarun, Fayum Depression, Egypt (Andrews, 1903).

HORIZON: Jebel el-Qatrani Fm., Early Oligocene (Andrews, 1903).

DIAGNOSIS: Known material supposedly differs from shells attributed to "*Stereogenys*" *cromeri* by having a broader and shorter nuchal bone, a U-shaped anal notch, a pentagonal intergular, and triangular humeral scales, but see discussion below.

REFERRED MATERIAL: BMNH R.3100, anterior plastral lobe; BMNH R.3120, ante-

rior plastral lobe; AMNH 5089, weathered shell.

PREVIOUS WORK: Reinach (1903b), Dacqué (1912), Williams (1954b), Lapparent de Broin (2000a).

DISCUSSION: The type specimen, as based on figures in Andrews (1903) and his description, is a relatively well-preserved and complete shell, allowing a reasonable description and reconstruction (fig. 85, based on Andrews, 1903: pl. 7). Although this shell may be lost, we summarize its morphology below because it remains as one of the better-known shell taxa from the Fayum region. In any case, there are no skull associations with this material, so it is not identifiable as *Stereogenys,* and there is no character set that allows a shell-based generic identification. The supposed differences between the relatively well-preserved shell material of *"Stereogenys" libyca* and the poorly preserved shell attributed to "*S.*" *cromeri* are minor and could easily be individual variation or preservational (R.C.W.).

DESCRIPTION: The carapace is low arched and oval, slightly expanded posteriorly. A strong lateral carina crosses the bridge peripherals, and the shell bulges outward in the area covered by the last vertebral scale. The trapezoidal nuchal bone is slightly indented anteriorly, similar to *Cordichelys antiqua,* and is about one and a half times wider than long. The first pair of costals meet on the midline behind the nuchal bone separating it from the neurals. There are seven neurals, the anterior ones longer than wide, the posterior ones wider than long. The first neural is pentagonal, the rest are hexagonal. The midline meeting of the eighth costals separates the seventh neural from the suprapygal. The suprapygal is a broadly rounded diamond with the long axis perpendicular to the midline. There is a small notch at the posterior end of the rectangular pygal bone, marking the sulcus separating the last two marginal scales. Eleven pairs of peripherals border the eight costal bones. Peripherals four to seven form the bridge, the fifth and sixth contact the mesoplastra. The posterior peripherals are more expanded than the anterior. According to Andrews (1906: 304) "both buttresses are weaker and less developed than in most pleurodires, the inguinal being the stronger of the two." The first of the five vertebral scales is relatively small and pentagonal. In contrast to the commoner condition in pleurodires, the first vertebral is narrower than the nuchal bone underlying it. The remaining vertebrals are hexagonal and much larger than the first. Marginal scales 1, 5, 7, 9, and 11 are pentagonal; the others are all quadrilateral.

The posterior lobe of the plastron is longer than the anterior lobe. The front margin of the anterior lobe is squared off and slightly concave. Andrews noted (1906: 304) that "The upper surface in this region is also gently concave from side to side, the concavity being bounded by thickened ridges borne on the epiplastrals and anterior part of the hyoplastrals." Differences in the shape of the entoplastron were cited by Andrews (1903: 119) as a means of distinguishing between *cromeri* and *libyca.* Although the entoplastron of *libyca* is smaller than that of *cromeri* it is the same shape. In view of the variability in the shape of this bone in some pleurodires (e.g., *fajumensis* Dacqué, 1912: fig. 7), the taxonomic significance of the entoplastron shape is questionable. The posterior extremity of the entoplastron extends past the level of the axillary notch. Small, hexagonal mesoplastra, longer than broad, are wedged between the distal extremities of the hyo- and hypoplastra. The anal notch is shallow and U-shaped. Parallel to the outer border of the posterior lobe, there is a ridge on the inner surface, which fades out midway along the xiphiplastron (Reinach, 1903b: pl. 13, fig. 9). The lateral surface of this ridge slopes gently outward, tapering to a thin edge. The scales of the plastron overlap onto the dorsal plastral surface to a greater extent than in the living podocnemidids. Wide separation of the small gular and humeral scales is related to the large, pentagonal intergular, extending posteriorly to the middle of the entoplastron. A sulcus separating the sixth marginal from the abdominal scale slants across the mesoplastron, but the pectoral scale does not reach the mesoplastron.

DESCRIPTION OF SHELL ATTRIBUTED BY ANDREWS (1906) TO *STEREOGENYS CROMERI*: Although we do not feel that there is any evidence to associate this shell with the skull of *Stereogenys cromeri*, or anything else,

it is worth discussing the interpretation that this shell is the same taxon as the shell-based *"S." libyca.*

The shell material of this presumed taxon is poorly preserved, and there is also ambiguity in the various Andrews descriptions as to which specimen he is describing. The carapace is oval, its greatest lateral expansion slightly anterior to the inguinal notch. There may have been an indentation along the anterior carapace margin. The nuchal illustrated (Andrews, 1906: fig. 96) is slightly broader than long. The total number of neurals cannot be determined, but seven is most likely, based on the reconstruction and the close similarity to the shells of *"S." libyca*. Instead of contacting the nuchal bone, the first neural is separated by the midline contact of the first costal bones. The first neural is pentagonal, the only other preserved one, probably the fifth, is hexagonal, as in the better preserved *"S." libyca.* The pygal is trapezoidal, and there are the usual eight pairs of costals, but the number of peripherals is indeterminate.

The plastron of "*Stereogenys*" *cromeri* has a bridge longer than the posterior lobe that is longer than the anterior lobe. The anterior lobe is more angular than rounded and its anterior edge is slightly concave. The epiplastra are broader laterally than at the midline giving the anterior lobe a squared-off shape. "In some specimens the upper surface of the epiplastrals is raised into a sort of boss near their posterior angle, and from this a slight ridge is continued backwards to the axillary buttress" (Andrews, 1906: 300). The external outline of the entoplastron, although poorly preserved, is variable in the available specimens. Being rhomboidal to escutcheon shaped in specimens described by Andrews (ibid.). Mesoplastron sutures are absent. "The posterior border of the plastron seems to have been notched in the middle line as in *St. libyca*, but in no specimen is this region well preserved" (Andrews, 1906: 300). And yet the anal notch shape was used to distinguish *cromeri* from *libyca.* Later work by one of us (R.C.W.) suggests that a specimen containing a left xiphiplastron (BMNH R.3200) shows that the anal notch is small and broadly V-shaped in contrast to "*S.*" *cromeri.* Little of the plastral scale pattern is preserved in the attributed material. There is a large, apparently, seven-sided intergular scale, although the actual difference between this and the large five-sided intergular of "*S.*" *libyca* is a matter of interpretation. The intergular scale extends posteriorly to the middle of the entoplastron and completely separates the humerals and the gulars. The gulars are small, triangular scales and the humerals are slightly larger and trapezoidal. Both are entirely on the epiplastra. No other scale markings are apparent in the available material.

### *Stupendemys* Wood, 1976

"*Stupendemys*" *souzai* Bocquentin and Melo, 2006

TYPE SPECIES: *Stupendemys geographicus* Wood, 1976.

DISTRIBUTION: Miocene of northern South America.

DIAGNOSIS (from Wood, 1976: 2): " Shell gigantic; carapace depressed, with irregular nodular contours on external surface and deep median notch at front; anterior border of nuchal bone thickened and moderately to strongly upturned; posterior peripheral bones moderately scalloped along margins; neurals arranged in uninterrupted sequence, numbers two through six hexagonal, the seventh pentagonal. Mesoplastra hexagonal to subcircular, largely confined to bridge; lateral ends of pectoral-abdominal scute sulci terminating just anterior to axial notches of shell." For further diagnostic characters of vertebrae and limbs, see Wood (1976: 2, 3).

DISCUSSION: Despite Bocquentin and Melo (2006), we do not recognize other species of *Stupendemys* fide Meylan et al. (2009). This is another well-diagnosed, distinct podocnemidid taxon that lacks a skull and has insufficient characters to be resolved in our character analysis. See discussion under *Caninemys* for why this shell is probably not that genus and in any case, there are no skull-shell associations.

### *Stupendemys geographicus* Wood, 1976

TYPE SPECIMEN: MCNC 244, medial portion of carapace, left femur, parts of scapulocoracoid, cervical vertebra (eighth?), Wood (1976: figs. 1, 3, 9).

TYPE LOCALITY: West of Quebrado Tio Gregorio, near town of Urumaco, Venezuela (Wood, 1976: 3).

HORIZON: "Upper member of Urumaco Formation" (Wood, 1976: 3). See also Gaffney and Wood (2002: 4), Sánchez-Villagra and Aguilera (2008), as well as entire number of *Paläontologische Zeitschrift* 82 (2) for more recent information on Urumaco Formation and its fauna.

DIAGNOSIS: As for genus.

REFERRED MATERIAL: Specimens described in Wood (1976) from type locality: MCZ 4376, shell and associated elements (Wood, 1976: pl. 1; Meylan et al., 2009: fig. 6, lower); MCNC 245, plastron and associated elements (Wood, 1976: fig. 2); MCZ 4377, cervical (Wood, 1976: fig. 3); MCZ 4378, humerus (Wood, 1976: fig. 8).

Specimens from late Miocene of southwestern Amazonia described in Gaffney et al. (1998): LACM 131946, nuchal (Gaffney et al., 1998: fig. 3); LACM 138028, right scapula (Gaffney et al., 1998: fig. 4); LACM 137948, cervical.

Other specimens identified as *Stupendemys* but disputed by Meylan et al. (2009) are described in Bocquentin and Negri (1993), Lapparent de Broin et al. (1993), Bocquentin and Melo (2006).

PREVIOUS WORK: Bocquentin and Negri (1993), Lapparent de Broin et al. (1993), Gaffney et al. (1998), Bocquentin and Melo (2006), Scheyer and Sánchez-Villagra (2007), Meylan et al. (2009), and Riff et al. (2010). Sánchez-Villagra and Scheyer (2010) provide an overview of the genus and nice restoration.

## TAXA NOMINA DUBIA

These are taxa that are invalid and not diagnosable for one reason or another.

### *Duerochelys arribasi* Jiménez, 1975

TYPE SPECIMEN: Faculty of Sciences of the University of Salamanca, Spain (Sala de las tortugas de la Universidad de Salamanca, Jiménez Fuentes, 1988), FCUS 326, a plastron.

TYPE LOCALITY: 15 kms west of Salamanca, Spain.

HORIZON: Ludien (Eocene).

DIAGNOSIS: See Jiménez Fuentes (1975). We do not note any diagnostic characters.

DISCUSSION: This taxon is not recognized in Lapparent de Broin's (2001) detailed compilation of European turtles, supporting our interpretation that the taxon is not diagnosable. The type consists of a plastron with a pair of intergular scales that divide the gulars and partially divide the humerals, a common variation in *Neochelys arenarum* (Broin, 1977: fig. 12). We see no features allowing this specimen to be differentiated from *Neochelys*. The specimen may demonstrate the presence of *Neochelys arenarum* in the Spanish Eocene.

### *Latisternon microsulcae* Auffenberg, 1981

TYPE SPECIMEN: Kenya National Museum F3532, a left epiplastron (figured Auffenberg, 1981: fig. 2).

TYPE LOCALITY: Olduvai Gorge, Tanzania (see Auffenberg, 1981: 512 for more information).

HORIZON: Pleistocene, Olduvai Group (see Auffenberg, 1981: 512 and Lapparent de Broin, 2000a: 68 for more discussion).

DIAGNOSIS: See Auffenberg (1981: 511, 512) for characters differentiating this epiplastron from some other epiplastra. The association of a nuchal bone (Kenya National Museum F4729; figured Auffenberg, 1981; fig. 3) is not certain.

DISCUSSION: This taxon is recognized by Lapparent de Broin (2000a: 68) as "Pelomedusoides indet. incertae familiae, ?Pelomedusidae" without comment. The type is inadequate for a reasonable diagnosis.

### *"Podocnemis" aegyptiaca* Andrews, 1900

TYPE SPECIMEN: CGM unnumbered, complete plastron and partial carapace (Andrews, 1900: pl. 1). Not seen.

TYPE LOCALITY: Moghara Oasis, eastern end of Qattara Depression, Egypt.

HORIZON: Moghara Fm., early Miocene (18–17 Ma; Miller, 1999).

DIAGNOSIS: Differs from all other podocnemidids in the shape of the second and third vertebral scales, which have lateral protrusions anterior to the pleural sulci and a sinuous sulcus with the adjacent pleural scale. The intergular scale is very small, barely

separating the large gular scales, which constrict the midline contact of the pectoral scales, virtually identical to that found in *Erymnochelys madagascariensis.*

Referred Material: A number of specimens have been referred to this species, although the basis for identifying some of the material that does not overlap morphologically with the type specimen is uncertain. BMNH R.2960, plastral fragment; BMNH R.2961, plastral and carapace fragments; CGM unnumbered, complete shell figured by Fourteau (1920: fig. 21) not seen by R.C.W. at CGM. Nonetheless, the partially inaccurate figure of Fourteau is important in that it apparently shows another individual with the vertebral scale character unique to *aegyptiaca* suggesting that the vertebral pattern is not an individual variation. Unfortunately, both this specimen and the type seem to be missing.

Previous Work: Andrews (1900), Dacqué (1912), Fourteau (1920), Williams (1954c).

Discussion: This species (fig. 87, based on Andrews, 1900, and Fourteau, 1920) seems to be adequately diagnosed in the literature, although the only two good specimens seem to be missing. The nearly identical scale pattern of the plastron in *aegyptiaca* and *Erymnochelys* led Williams (1954c) to place *aegyptiaca* in that genus. The frequently conservative nature of Pelomedusoides shells makes this conclusion difficult to confirm without associated skull material.

### *"Podocnemis" bramlyi* Fourteau, 1920

Type Specimen: An unnumbered plastron with parts of right side of carapace attached (Fourteau, 1920: fig. 23). According to Fourteau (1920: ix), the specimen is in the CGM collection, but it could not be found by one of us (R.C.W.) in the 1960s.

Type Locality: Moghara Oasis, Egypt (Fourteau, 1920).

Horizon: Moghara Fm., early Miocene (Fourteau, 1920; Miller, 1999).

Diagnosis: Again, the only character for this taxon lies in the scale pattern of the anterior plastral lobe. In this case, the intergular scale separates the small, triangular gular scales and contacts and partly separates the humerals. The intergular is entirely on the entoplastron.

Discussion: The scale pattern in *bramlyi* is common in South American podocnemidids (e.g., *Peltocephalus, Podocnemis erythrocephala*) and led Williams (1954c) to suggest *bramlyi* as the ancestor of *Peltocephalus.* However, the scale pattern on the anterior lobe of podocnemidid shells is inadequate as the sole source of characters to determine phylogenetic relationships in this group due to intraspecific variability.

Another question, however, is whether or not *bramlyi* could be the shell for the skull-based *Mogharemys,* as they are from the same unit. There is no suggestion of physical association, although the locality data for both known specimens of *bramlyi* and *Mogharemys* is so inadequate that they could be from the same place. The only character present in *bramlyi* allies it with the magnatribe Eymnochelydand, which also includes *Mogharemys*, so it is possible. At present, however, *bramlyi* remains a nomen dubium.

### *"Podocnemis" brasiliensis* Staesche, 1937

*Bauruemys brasiliensis* (Staesche, 1937) Kischlat, 1994

Type Specimen: DGM 214-R in Price (1953: 12) but DGM 2980 in Candeiro et al. (2006: 927). Correct number is MCT 214-R (G.R. Oliveira, personal commun.). Partial plastron figured in Staesche (1937: fig. 1 [restored], pls. 16, 17) and Price (1953: figs. 1, 2.).

Type Locality: Araçatuba Jupia, Mirandópolis, São Paulo State, Brazil.

Horizon: Adamantina Fm. fide Candeiro et al. (2006).

Diagnosis: Although diagnoses are given by both Staesche (1937) and Price (1953), these do not actually distinguish this taxon from many others known today.

Referred Material: None.

Previous Work and Discussion: The type is inadequate for an objective diagnosis, and Oliveira and Romano (2007) correctly considered it a nomen dubium.

### *"Podocnemis" freibergi* Agnolin, 2004

Type Specimen: MACN PV 18243, fragment of anterior carapace.

TYPE LOCALITY: Near Andalhuala, Santa María, Catamarca Province, Argentina (Agnolin, 2004).

HORIZON: Andalhuala Fm., Late Miocene (Agnolin, 2004).

DIAGNOSIS: See Agnolin (2004) for inadequate diagnosis.

REFERRED MATERIAL: None.

PREVIOUS WORK: None.

DISCUSSION: The diagnosis and description do not distinguish this carapace fragment from a number of possible pelomedusoides. It is a nomen dubium.

### *"Podocnemis" harrisi* Pacheco, 1913

*Roxochelys harrisi* (Pacheco, 1913) Broin, 1991
*Roxochelys harrisi* (Pacheco, 1913) Candeiro et al., 2006

TYPE SPECIMEN: DGM 287, right xiphiplastron and three peripherals, Pacheco (1913: text fig. 6, pl. 3, fig. 6a–6e), "all of which appear to be lost at present" (Candeiro et al., 2006: 927).

TYPE LOCALITY: Colina, São Paulo State, Brazil.

HORIZON: Adamantina Fm. fide Candeiro et al. (2006).

REFERRED MATERIAL: None.

PREVIOUS WORK AND DISCUSSION: Price (1953) raised the issue of similarity between *harrisi* and *wanderleyi*, which was formalized by Broin (1988, 1991) and Kischlat (1994), both of whom referred these species to *Roxochelys*. The species *harrisi* itself has never had reasonable material added to the type specimens, which are undiagnosable by any objective criteria. Oliveira and Romano (2007) considered it a nomen dubium.

### *"Stereogenys" podocnemoides* Reinach, 1903b

*Podocnemis podocnemoides* (Reinach) Schmidt, 1940
"Erymnochelyinae indet. Genus indet. (*Neochelys* group?: '*Stereogenys*') *podocnemoides*" Lapparent de Broin, 2000a

TYPE SPECIMEN: An unnumbered plastron (Reinach, 1903b: pl. 10) in the Bayerische Staatssammlung für Paläontologie und historische Geologie in Munich. Not seen, apparently lost in World War II (Crumly, 1984).

TYPE LOCALITY: Northwest of Lake Qarun, near "Dime" (Reinach, 1903b)

HORIZON: "Obere Mitteleocän," probably Qasr el-Sagha Fm., Late Eocene.

DIAGNOSIS: The only diagnostic character likely to be useful at this point is the anterior lobe of the plastron, which shows a long, narrow intergular scale separating both gular and humeral scales. The carapace, not part of the type but associated with it by Reinach (1903b: pl. 11, fig. 1), does not show the supposedly diagnostic character of the shell attributed to *"Stereogenys,"* the separation of the first neural from the nuchal.

DISCUSSION: This species must be considered to consist only of the type plastron as there is no evidence that it was part of the same individual as the referred carapace. The plastron apparently comes from the Eocene Qasr el-Sagha Fm. and is a possible candidate for the shell specimens in the DPC from the same unit, rather than the Oligocene *fajumensis* that we have chosen. It is possible that the type specimen of "*Stereogenys*" *podocnemoides* Reinach is in fact the same species as the DPC material, but difficult to demonstrate with the present material. In the first place, the type specimen, even if it still existed, is inadequate to diagnose a podocnemidid species in our opinion. Secondly, there is variation in the known Oligocene specimens of *fajumensis*, including an articulated set of epiplastra and entoplastron (AMNH 5093) that has a long intergular scale separating the gulars and reaching (but not separating as in *podocnemoides*) to the humeral scales. Thirdly, there are a number of Eocene *Neochelys* from Europe that have this exact pattern (Broin, 1977: figs. 12, 22). Nonetheless, there are no known specimens of Oligocene *fajumensis* or of DPC specimens here identified as *fajumensis* that actually have the scale pattern shown in the type of *podocnemoides*. But it is still probably *Neochelys*.

It would be best to recognize "*Stereogenys podocnemoides*" Reinach, 1903b, as a nomen dubium.

## CRANIAL MORPHOLOGY OF *LAPPARENTEMYS*, *PRICEMYS*, *PEIROPEMYS*, AND *BAURUEMYS*

Figures 7–34

PREFRONTAL (figs. 7, 10, 12, 14, 15, 18, 19, 22, 23, 25)

**Contacts:** The prefrontal contacts are very similar in most of the podocnemidids, as in *Peiropemys*, *Bauruemys*, and *Lapparentemys*: with the other prefrontal on midline, the maxilla anteroventrolaterally, and the frontal posteriorly. There is no anteroventral contact with the palatine. The bone is unknown in *Pricemys*.

**Structures:** The dorsal margin of the apertura narium externa does not protrude in *Bauruemys*, but it does in *Lapparentemys* and *Peiropemys*. It is variable in the living *Podocnemis*, *P. expansa* tends to have a distinct protrusion, as do many specimens of *P. erythrocephala*, but many other specimens of *Podocnemis* have a flatter margin. This seems to be a character very subject to individual variation, at least in *Podocnemis*. The interorbital distance is about the same in *Peiropemys*, *Lapparentemys*, and *Bauruemys*, and this is slightly wider than in *Podocnemis*. *Podocnemis* has the midline sulcus in all species we recognize, and this is formed on the prefrontals and frontals. In *Peiropemys*, *Lapparentemys,* and *Bauruemys*, the interorbital surface is convex without any indication of a sulcus or depression.

The sulcus olfactorius on the ventral surface of the prefrontal is relatively narrow in *Peiropemys*, *Lapparentemys*, and *Bauruemys*, as it is in *Podocnemis*. The ventral process of the prefrontal forms the anterior edge of the widely open foramen orbito-nasale, a poorly defined structure in these podocnemidids, widely confluent with the fossa nasalis.

FRONTAL (figs. 7, 10, 12, 14, 15, 18, 19, 22, 23, 25)

**Contacts:** The frontal contacts in *Peiropemys*, *Bauruemys*, and *Lapparentemys* are all the same as in *Podocnemis* and are similar in all podocnemidids. The frontal contacts the other frontal on the midline, the prefrontal anteriorly, the postorbital posterolaterally (except on the surface in some *Podocnemis expansa* fide Ruckes, 1937), and the parietal posteriorly. The degree of contact varies, however. In *Lapparentemys*, *Bauruemys*, and *Peiropemys*, there is a longer contact with the postorbital than in *Podocnemis*. In *Podocnemis* the postorbital is unusually small compared with the other podocnemidids. In *Podocnemis sextuberculata* the postorbital is particularly small and may have no exposure on the skull roof (Ruckes, 1937; although according to G.R. Oliviera, personal commun., some of Ruckes's specimens were incorrectly identified). The frontal is missing in *Pricemys*.

**Structures:** The frontal forms the posteromedial margin of the orbit, and is of about the same relative size in *Lapparentemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis*. On the ventral surface the sulcus olfactorius is a low ridge developed to about the same extent in all four of these taxa. *Podocnemis* is differentiated from the other podocnemidids by the midline sulcus or interorbital groove on the dorsal surface of the prefrontals and frontals.

PARIETAL (figs. 7, 10, 12, 14, 15, 18, 19, 22, 23, 25, 26, 29)

**Contacts of dorsal plate:** The parietal in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* have the same contacts: the other parietal on the midline, the frontal anteriorly, the postorbital anterolaterally, and the quadratojugal laterally. *Podocnemis* differs from the other four in having a much narrower postorbital contact that exposes the edge of the jugal, which contacts the parietal anterolaterally between the postorbital and quadratojugal.

**Structures of dorsal plate:** The temporal emargination formed by the posterior rim of the parietal is more extensive in *Bauruemys* than it is in *Lapparentemys*, *Pricemys, Peiropemys*, and *Podocnemis*. However, this margin does vary in all these forms so this may not be particularly significant. Nonetheless, the available skulls of *Bauruemys* with preserved posterior temporal margins consistently show a slightly greater degree of temporal emargination than in *Lapparentemys*, *Pricemys, Peiropemys*, and all recent *Podocnemis* that we have seen. This can be seen in the relative lengths of the parietal-quadratojugal suture. *Lapparentemys* and *Peiropemys* show a slightly greater amount of emargination than in *Podocnemis*.

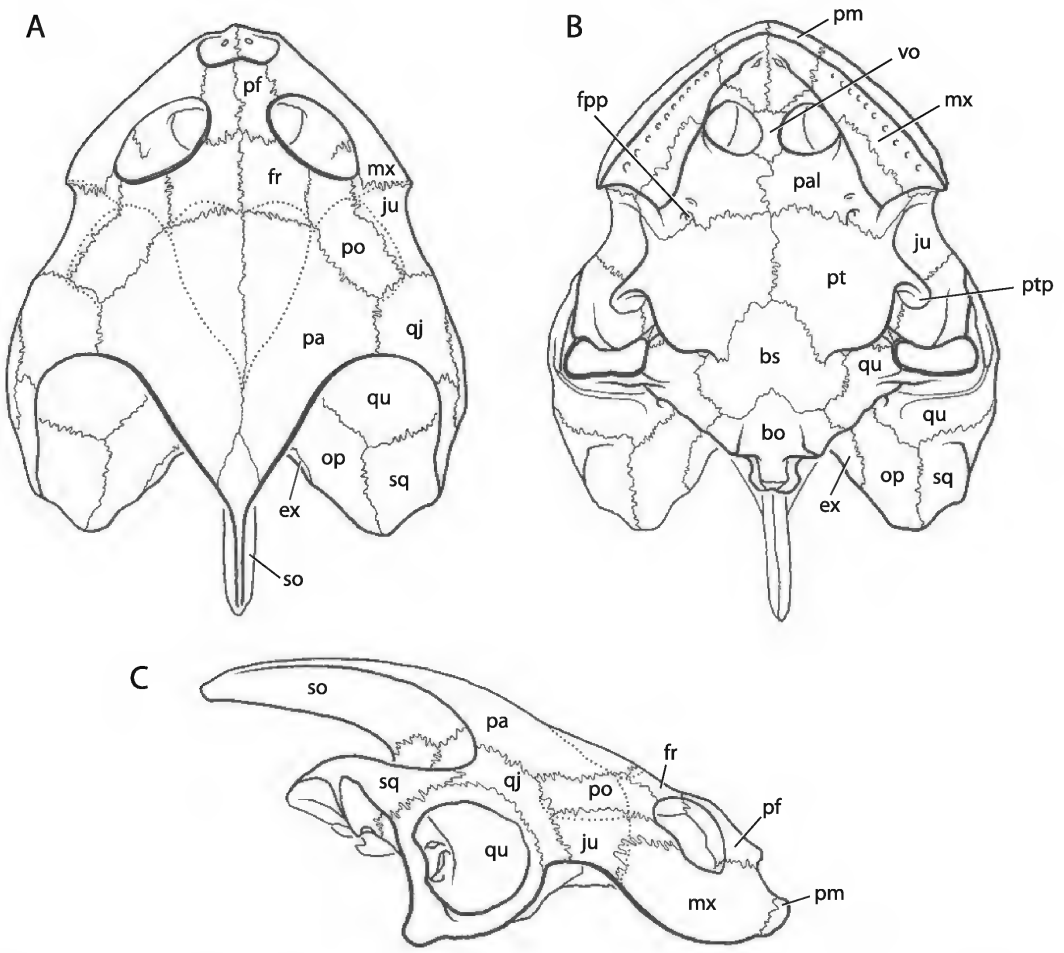



Fig. 7. *Bauruemys elegans* (Suárez,1969a). Partially restored skull based on DGM MCT 1492-R, DGM uncat A, MCZ 4123. **A,** dorsal; **B,** ventral; **C,** lateral. [A. Venjara, del.]

The ventral process lateral to the sulcus palatinopterygoideus is visible in *Peiropemys*, *Lapparentemys*, and *Bauruemys*, and it is similar in size and shape to that structure in *Podocnemis*. As in *Podocnemis*, the contact in *Lapparentemys*, *Peiropemys*, and *Bauruemys*, is with the postorbital laterally. In some species of *Podocnemis* (*P. expansa, P. sextuberculata, P. lewyana*), there is also a ventral contact with the pterygoid just above the processus trochlearis pterygoidei.

**Contacts of processus inferior parietalis:** In *Lapparentemys*, *Bauruemys*, *Pricemys,* and *Peiropemys*, the parietal contacts the pterygoid ventrally, the prootic posteroventrally, the supraoccipital posteriorly, and the palatine anteroventrally (just barely), as in *Podocnemis.*

**Structures of processus inferior parietalis:** The processus is quite similar in *Lapparentemys*, *Bauruemys*, *Pricemys*, *Peiropemys*, and *Podocnemis,* except for the considerably smaller size of the postorbital in *Podocnemis* and the related extension of surrounding bones into those areas usually occupied by the postorbital. The foramen interorbitale and the size and shape of the processus inferior parietalis are very similar in *Lapparentemys*, *Bauruemys*, *Pricemys*, *Peiropemys*, and *Podocnemis.* The foramen nervi trigemini in *Lapparentemys*, *Bauruemys*, *Pricemys*, *Peiropemys*, and *Podocnemis* has the usual three bones forming its margin: the parietal anterodorsally, the prootic dorsolaterally, and the pterygoid ventrally.

Fig. 8. *Bauruemys elegans* (Suárez, 1969a). Partially restored ventral view based on DGM MCT 1492-R and MCZ 4123. [A. Venjara, del.]

JUGAL (figs. 7, 10, 12, 14, 15, 18, 19, 22, 23, 25, 26, 31).

**Contacts of lateral plate:** In *Lapparentemys*, *Bauruemys*, and *Peiropemys*, the jugal has the usual generalized pleurodire contacts with the maxilla anteroventrally, the postorbital dorsally, and the quadratojugal posterodorsally. In *Pricemys* the jugal contacts the maxilla but its other contacts are missing. In *Podocnemis* the jugal is much larger and, due to the small postorbital, contacts the parietal and sometimes the frontal (Ruckes, 1937).

**Structures of lateral plate:** In *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and

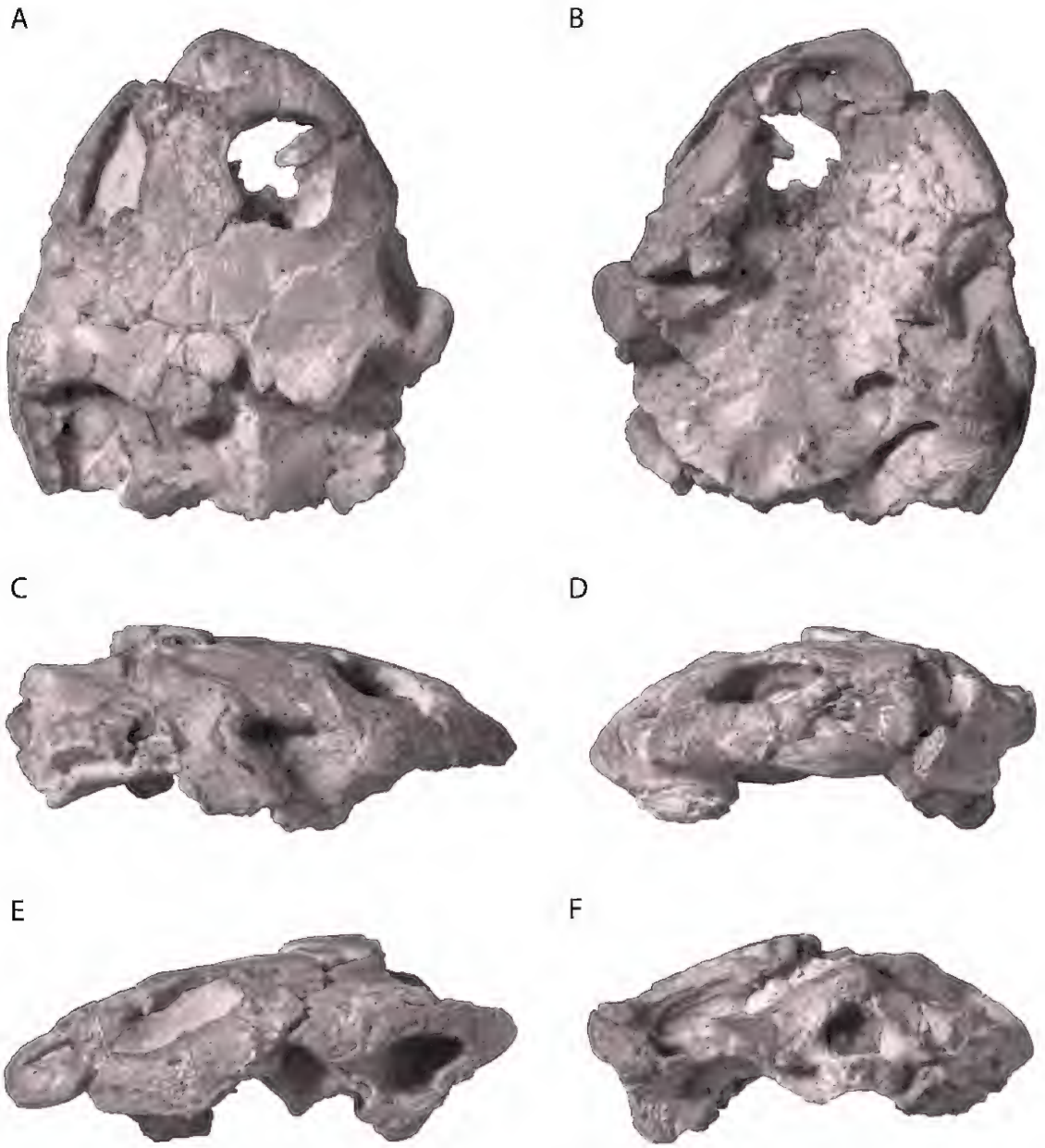



Fig. 9. *Bauruemys elegans* (Suárez,1969a). DGM MCT 1492-R, skull of holotype. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [C. Facella del.]

*Podocnemis* the jugal enters the orbital margin, forming its posteroventral edge. Some degree of cheek emargination formed by the maxilla, jugal, quadratojugal, and quadrate is present in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis.* However, the extent of the emargination varies among these taxa. *Lapparentemys* and *Peiropemys* have the most extensive emargination, while the best-preserved *Bauruemys* specimens (e.g., MCZ 4123) show slightly less emargination. This seems to be within the extent of variation seen in recent *Podocnemis* species. *Podocnemis* itself shows differences among its recent

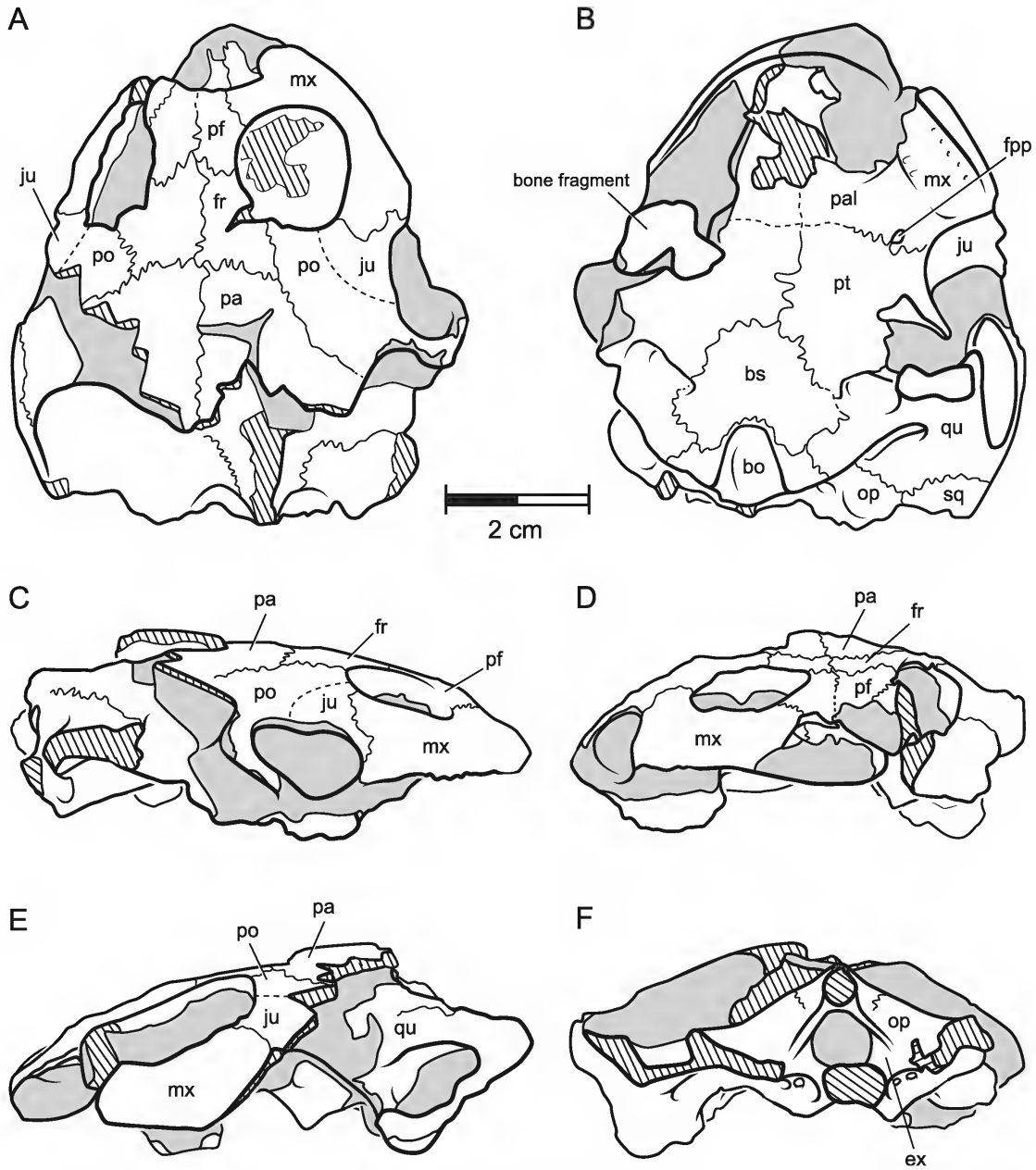



Fig. 10. *Bauruemys elegans* (Suárez,1969a). DGM MCT 1492-R, skull of holotype. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [C. Facella, del.]

species, with *unifilis* being slightly more emarginated than the other species.

**Contacts of medial process:** In the floor of the orbit (dorsal view) in *Lapparentemys*, *Pricemys*, *Peiropemys, Bauruemys*, and *Podocnemis*, the jugal contacts the maxilla anteriorly and laterally and the palatine medially. In *Podocnemis* the extent of jugal exposure in the orbital floor varies. In *P. expansa* (Gaffney, 1979: fig. 54) the jugal is largely restricted to the posterior wall of the fossa orbitalis, but in *P. sextuberculata* (Meylan collection 1013), *P, unifilis* (AMNH 58199), and *P. erythrocephala* (AMNH

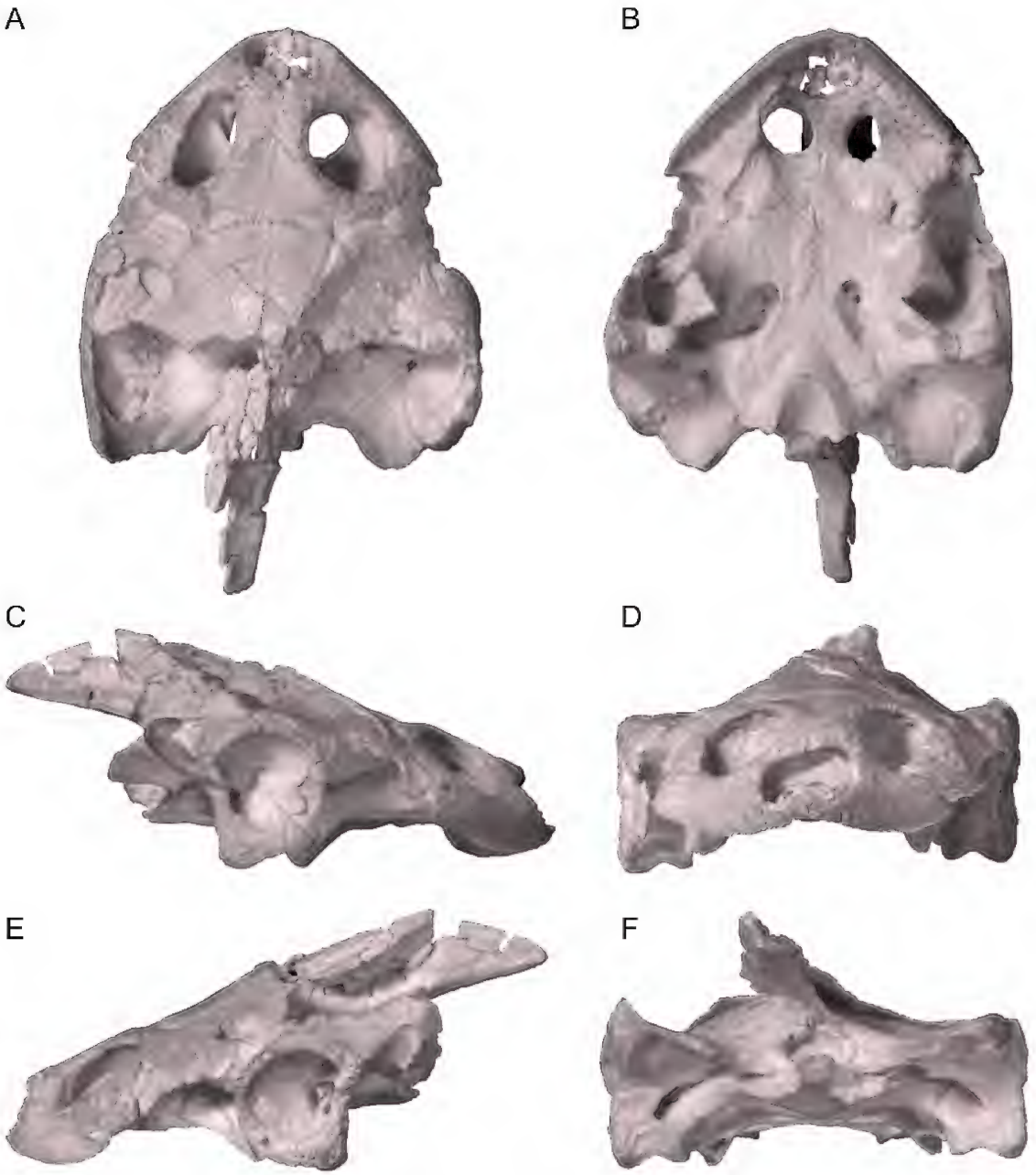



Fig. 11. *Bauruemys elegans* (Suárez,1969a). DGM MCT 1753-R. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [M. Vabulas, del.]

111070), the jugal sends a process anteriorly alongside the maxilla exposure. However, there seems to be individual variation in this genus in this feature and our sample of *Podocnemis* is too small to determine the range.

The contacts of the jugal are basically very similar in *Lapparentemys*, *Peiropemys*, and *Bauruemys*, but these vary from *Podocnemis* in relation to the large size of the jugal and the small postorbital. The contacts of the jugal in the septum orbitotemporale of

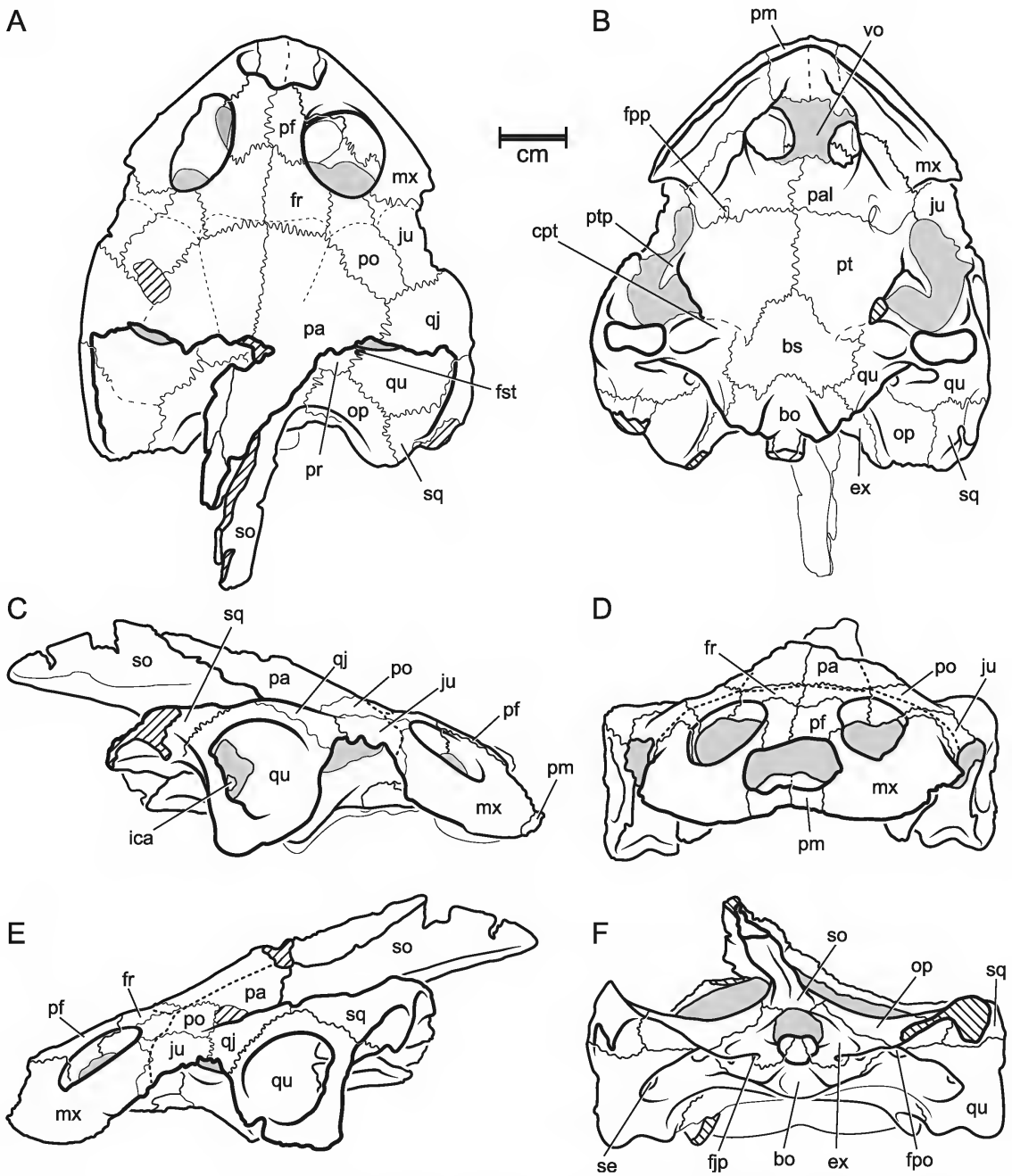



Fig. 12. *Bauruemys elegans* (Suárez,1969a). DGM MCT 1753-R. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [M. Vabulas, del.]

*Lapparentemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* are with the postorbital dorsomedially, the maxilla ventrally, the palatine ventromedially, and, in posterior view, the pterygoid medially. In the species and individuals of *Podocnemis* in which the postorbital is very small, the jugal also contacts the frontal dorsomedially.

**Structures of medial process:** The medial jugal process forms the posterior wall and

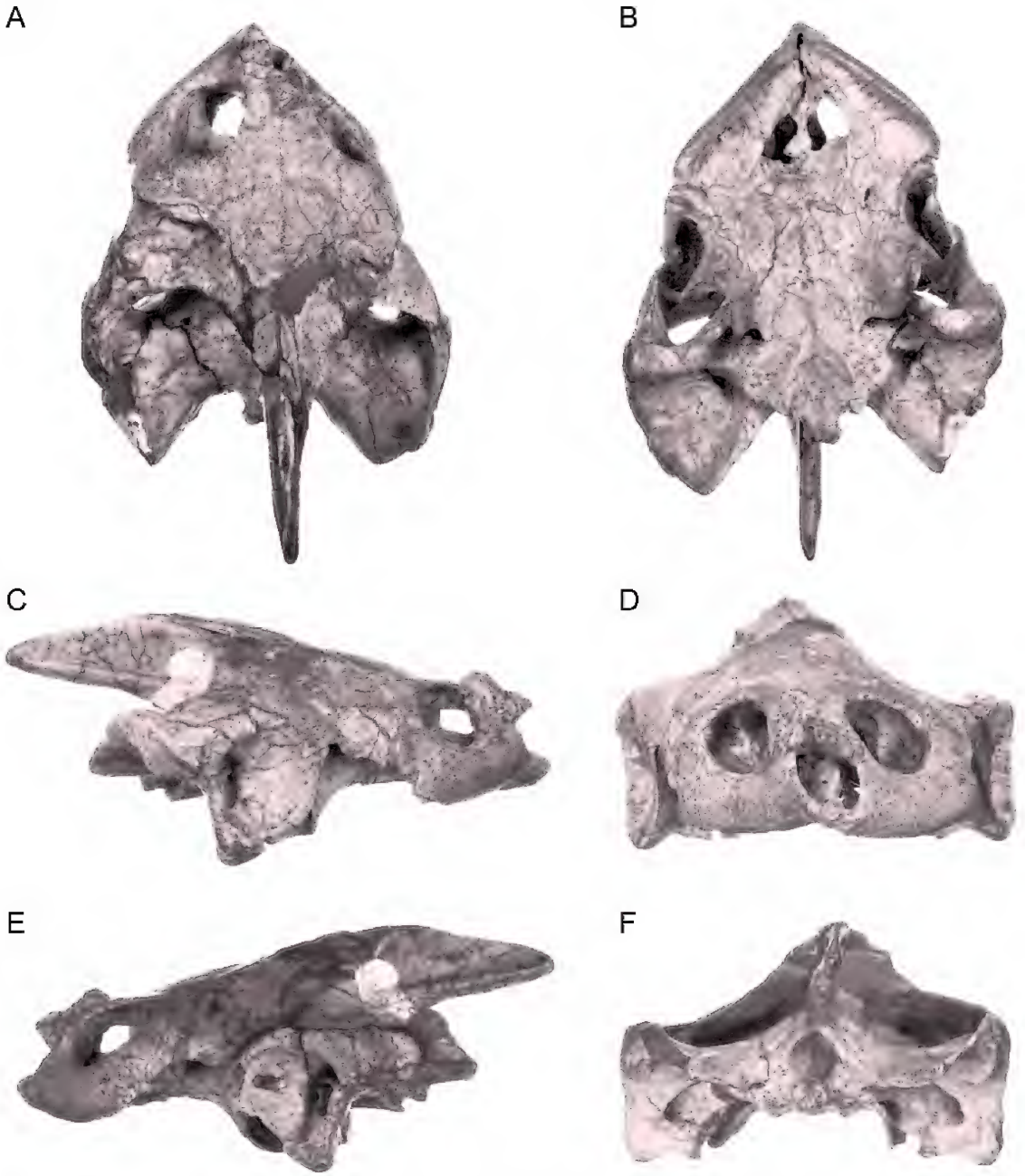



Fig. 13. *Bauruemys elegans* (Suárez, 1969a). MCZ 4123. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [A. Venjara, del.]

some of the floor of the fossa orbitalis in *Lapparentemys*, *Bauruemys*, *Pricemys,* and *Peiropemys*, but as described above, in *Podocnemis* some species have the process forming more of the floor. The septum orbitotemporale in *Lapparentemys*, *Bauruemys*, and *Peiropemys* has the usual pelomedusoides jugal component dorsolaterally; in *Podocnemis* this contribution is present, but usually more extensive medially as a function of the smaller postorbital.

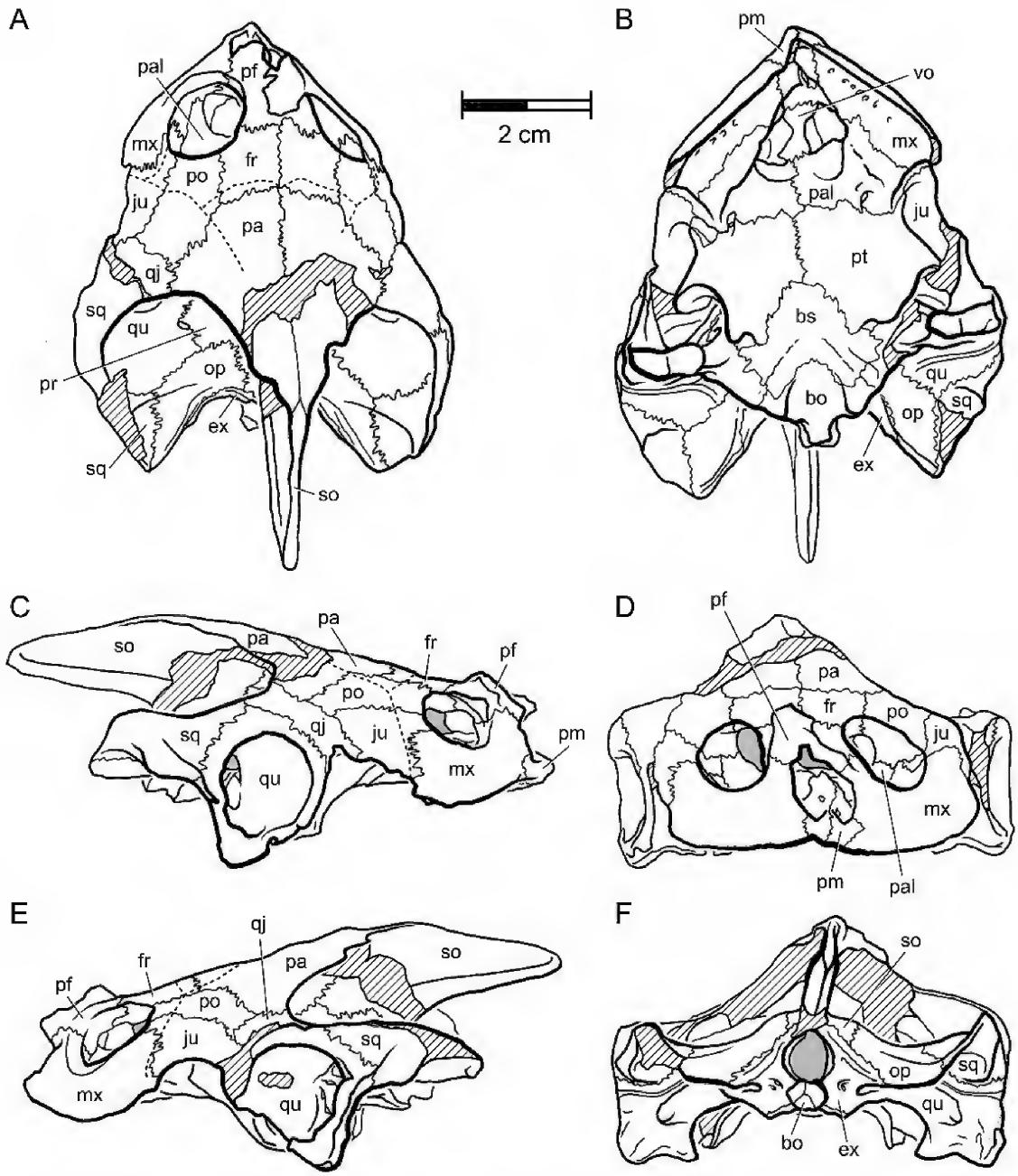



Fig. 14. *Bauruemys elegans* (Suárez, 1969a). MCZ 4123. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [A. Venjara, del.]

QUADRATOJUGAL (figs. 7, 10, 12, 14, 15, 18, 19, 22, 23, 25, 26, 29)

**Contacts:** In *Lapparentemys*, *Peiropemys*, and *Bauruemys*, the quadratojugal contacts the parietal medially, the quadrate posteroventrally, the squamosal posterodorsally, the postorbital anterodorsally, and the jugal anteroventrally. In *Pricemys* only the parietal, quadrate, and squamosal contacts are preserved and they agree with those in *Lapparentemys*. Except for differences in the degree of cheek and temporal emargination,

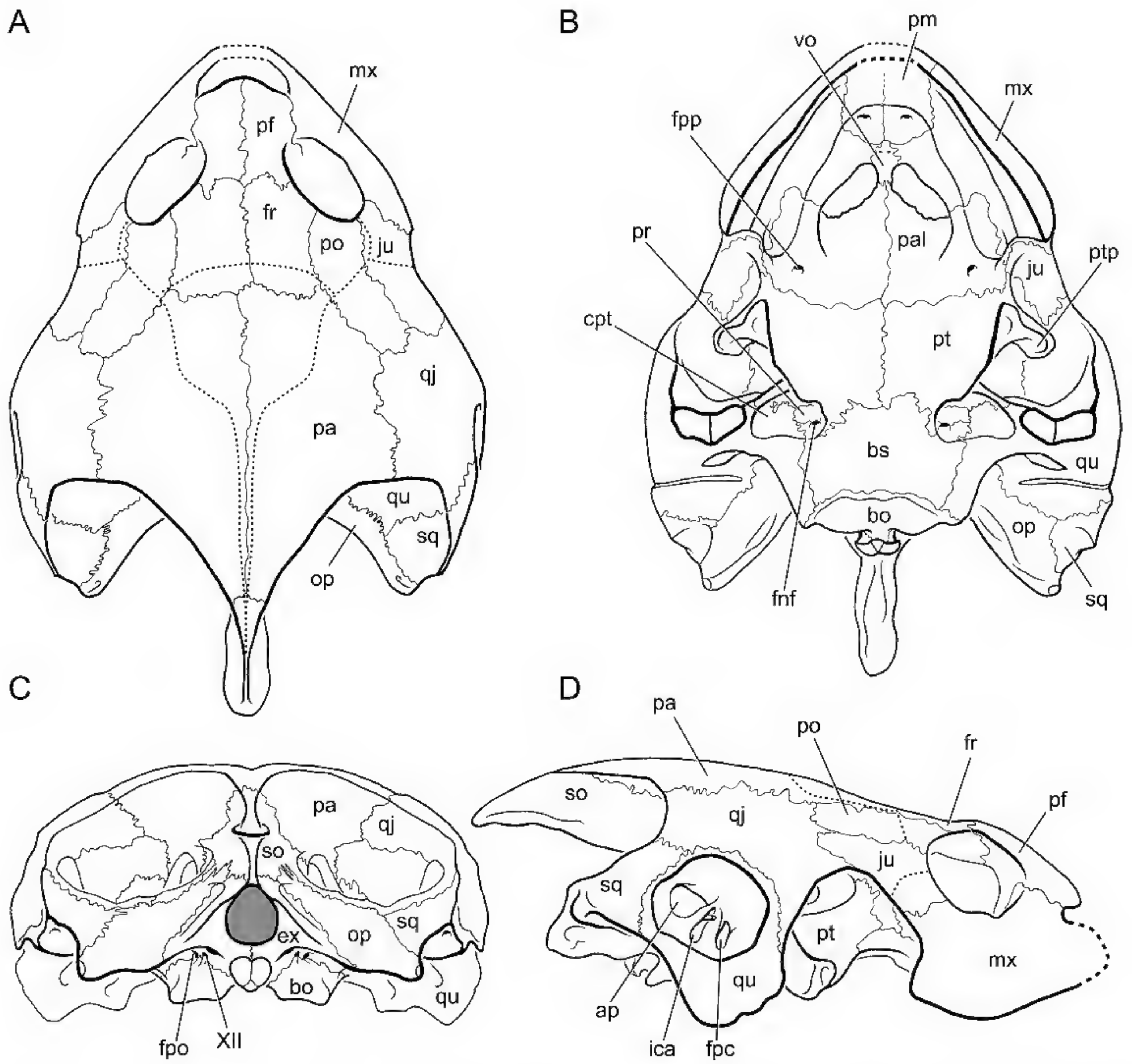



Fig. 15. *Peiropemys mezzalirai,* n. gen. et sp. Partially restored skull of holotype, DGM MCT 1497-R. **A,** dorsal; **B,** ventral; **C,** occipital; **D,** lateral. [P. Sloan, del.]

these contacts are similar in all these taxa. *Podocnemis* differs from the above by lacking the postorbital contact, due to the small size of the postorbital and the larger size of the jugal, which has a longer quadratojugal contact in *Podocnemis.*

**Structures:** The C-shaped quadratojugal is similar in size and shape in *Lapparentemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis.* The differences are related to the degree of emargination, cheek and temporal. The slightly greater temporal emargination of *Bauruemys* is associated with a slightly smaller quadratojugal than in *Lapparentemys*, *Peiropemys*, and *Podocnemis.*

SQUAMOSAL (figs. 7, 10, 12, 14, 15, 18, 19, 22, 23, 25, 26, 29, 33)

**Contacts:** As in other pelomedusoids, the squamosal contacts in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* are with the quadrate anteriorly and anteromedially, the opisthotic medially on the dorsal, posterior, and ventral surfaces, and the quadratojugal anterodorsolaterally.

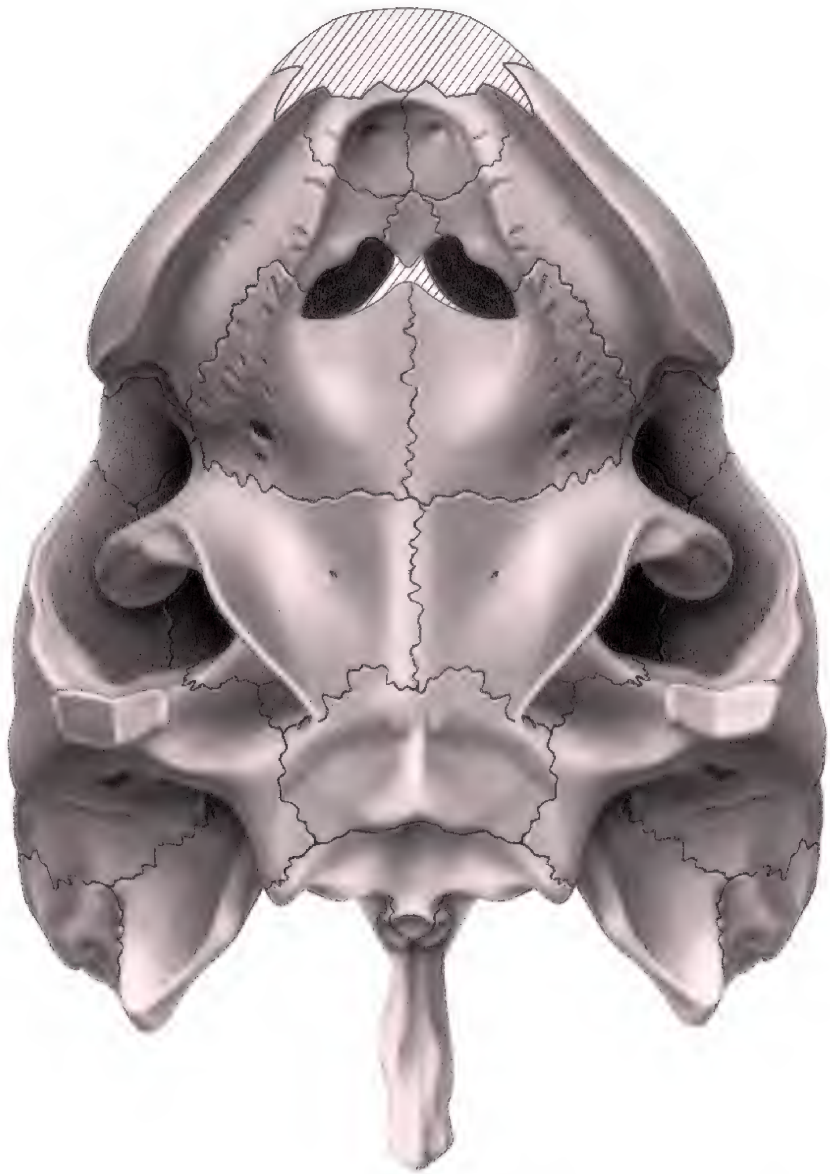


Fig. 16. *Peiropemys mezzalirai,* n. gen. et sp. Partially restored ventral view of skull DGM MCT 1497-R. [V. Storfer, del.]

**Structures:** As in other pelomedusoides the squamosal in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* is a cone-shaped bone fitting around the antrum postoticum of the quadrate. Among these four taxa, the squamosal shows little variation.

POSTORBITAL (figs. 7, 10, 12, 14, 15, 18, 19, 22, 23, 25)

**Contacts of lateral plate:** As in other pelomedusoids the postorbital in *Lapparentemys*, *Peiropemys*, and *Bauruemys* contacts the frontal anteromedially, the jugal ventrally, the quadratojugal posteriorly, and the parietal posteromedially. In *Podocnemis* the postorbital is always smaller to some extent than in *Lapparentemys*, *Peiropemys*, and *Bauruemys*, so the postorbital-quadratojugal

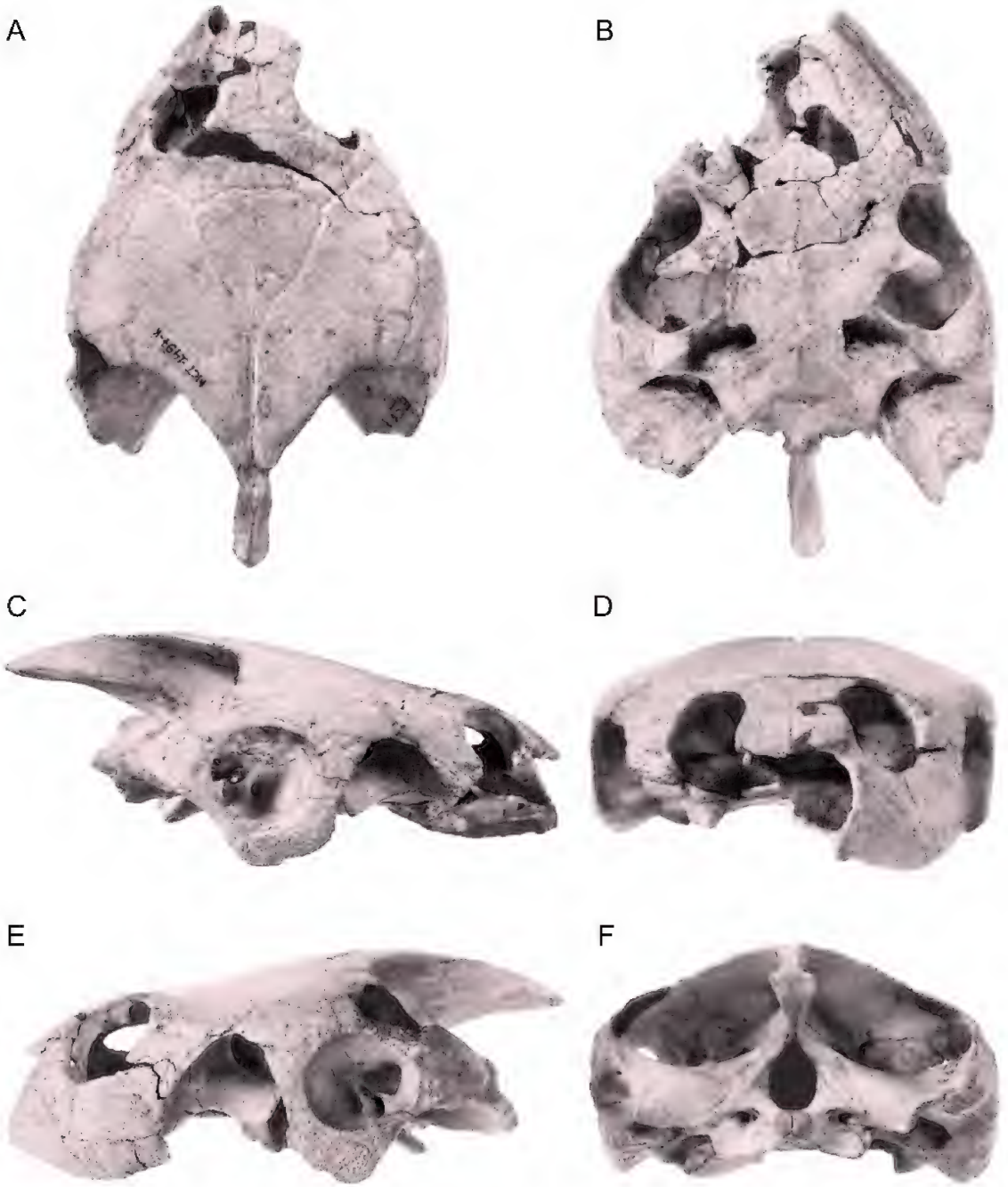



Fig. 17. *Peiropemys mezzalirai,* n. gen. et sp. DGM MCT 1497-R. Skull. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [P. Sloan, G. Giardina, del.]

contact is absent. The postorbital is missing in *Pricemys*.

**Structures of lateral plate:** In *Lapparentemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* the postorbital forms the posterodorsal part of the orbital margin and part of the skull roof. In *Podocnemis* the smaller size of the postorbital is characteristic of the genus,

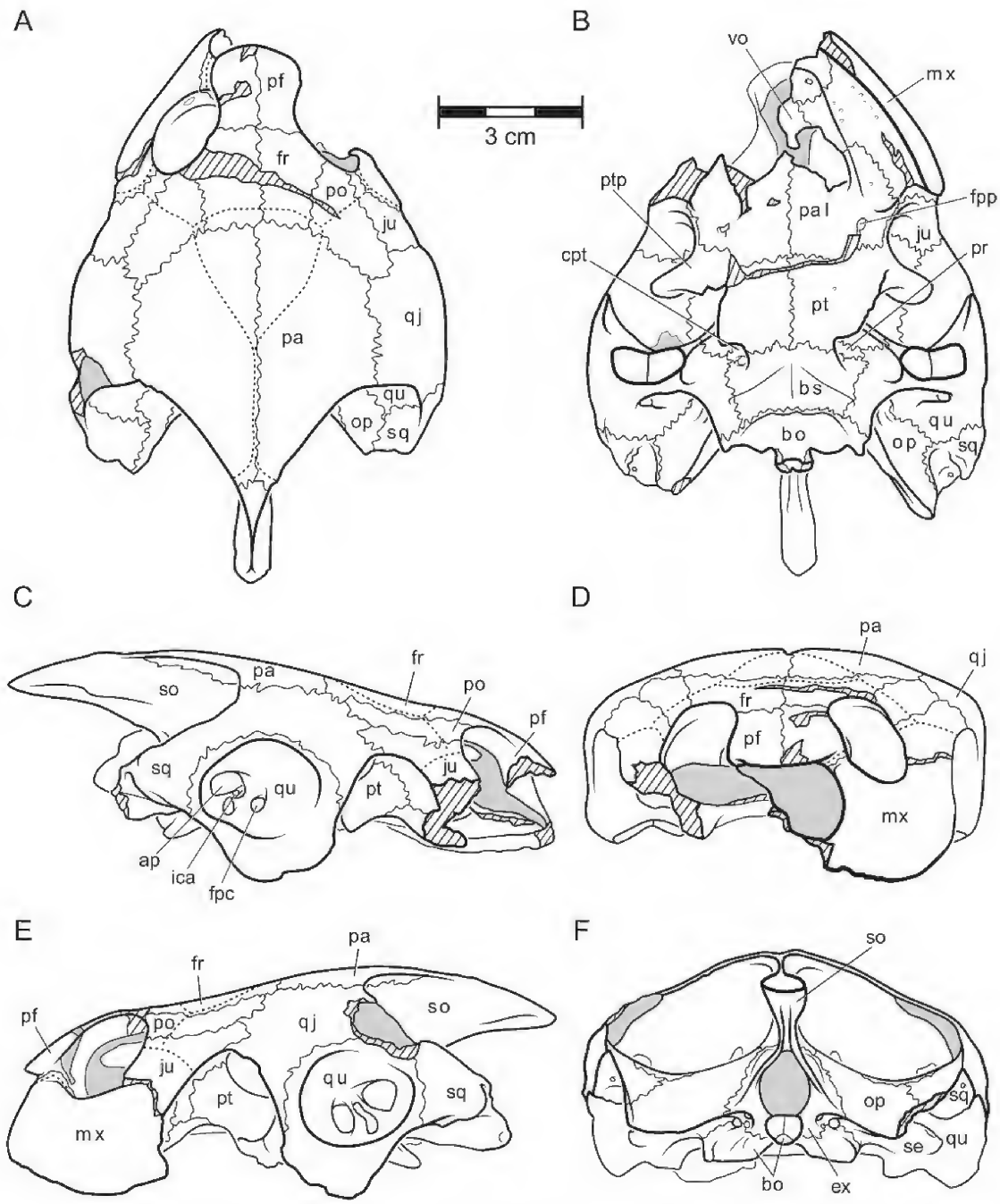



Fig. 18. *Peiropemys mezzalirai,* n. gen. et sp. DGM MCT 1497-R. Skull. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [C. Facella, del.]

but there is variation in the smal size within and among its species. All *Podocnemis* do have a postorbital that is half or less the size of the postorbital in *Lapparentemys*, *Peiropemys*, and *Bauruemys*.

**Contacts of medial process:** In *Lapparentemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis*, the postorbital contacts the frontal dorsomedially, the palatine ventrally, and the jugal ventrolaterally in the anterior surface of

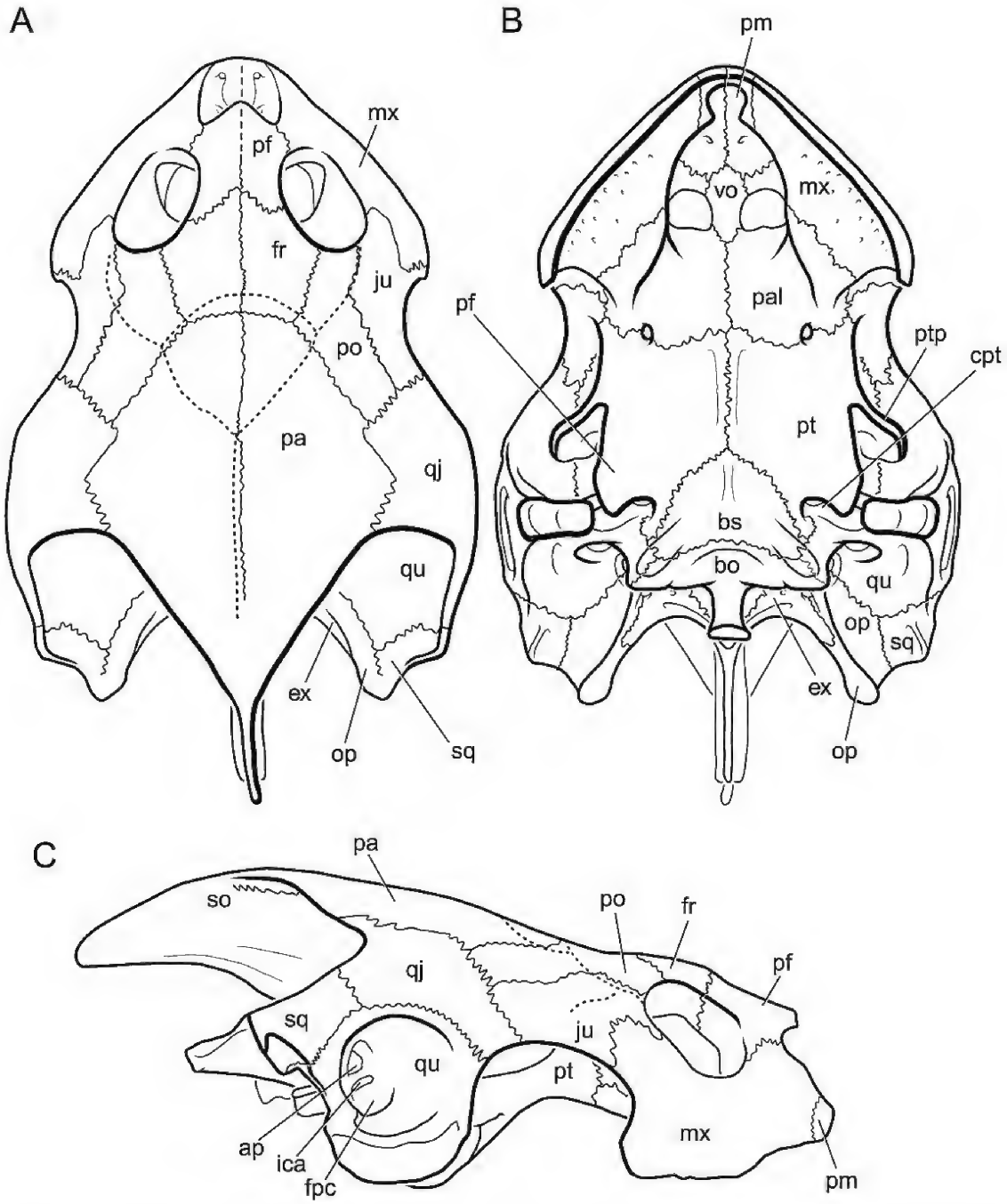



Fig. 19. *Lapparentemys vilavilensis* (Broin, 1971), n. gen. Partially restored skull based on AMNH 14444 and WUS 2160. **A,** dorsal; **B,** ventral; **C,** lateral. [F. Ippolito, del.]

the septum orbitotemporale, facing the fossa orbitalis. Even in *Podocnemis* that have the postorbital not exposed /retracted on the skull roof, it remains in the anterior surface of the septum orbitotemporale. In *Lapparentemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis*, as seen in the posterior surface of the septum orbitotemporale, facing the fossa temporalis,

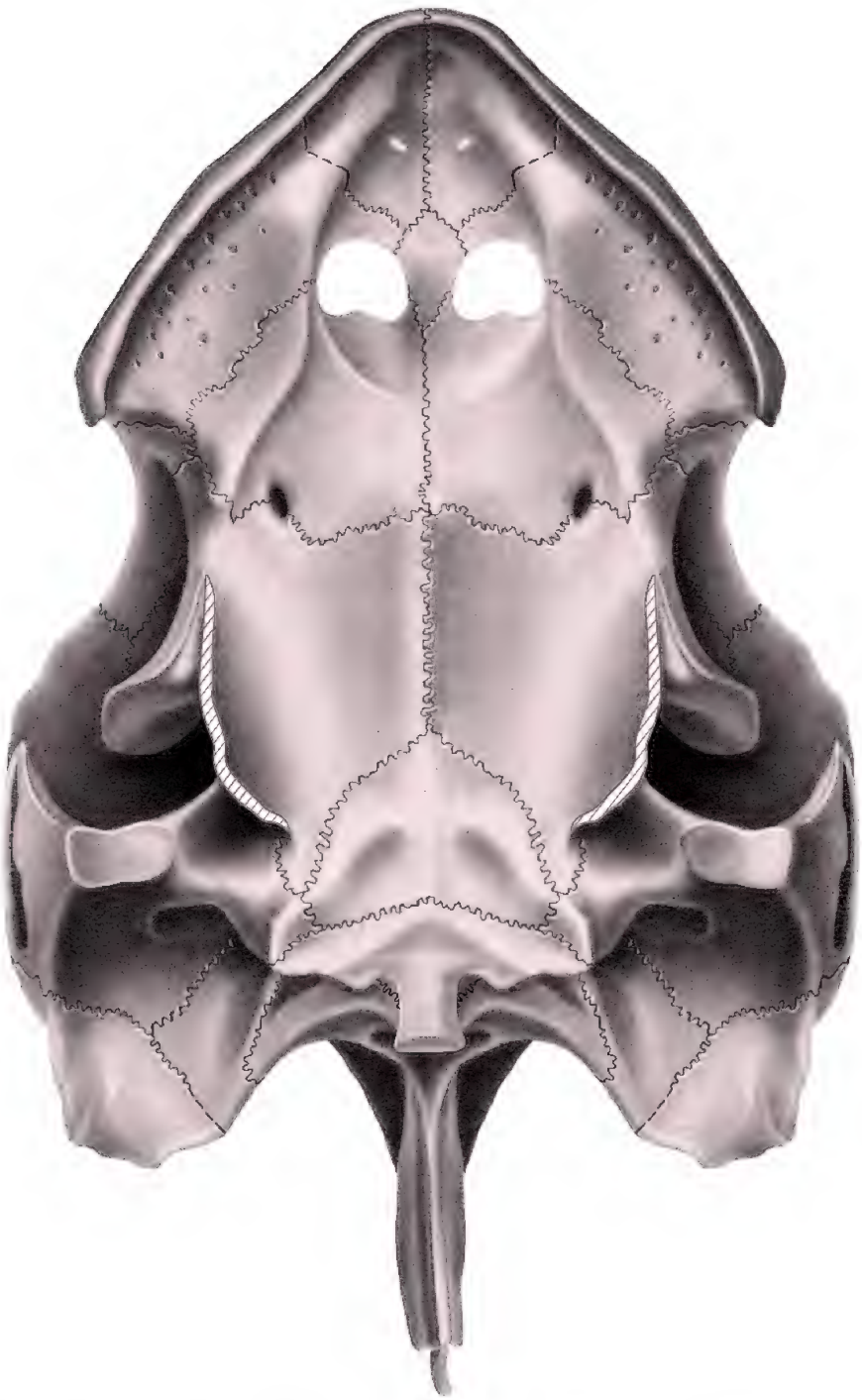


Fig. 20. *Lapparentemys vilavilensis* (Broin, 1971), n. gen. Partially restored ventral view of skull based on AMNH 14444. [T. Tarpley, del.]

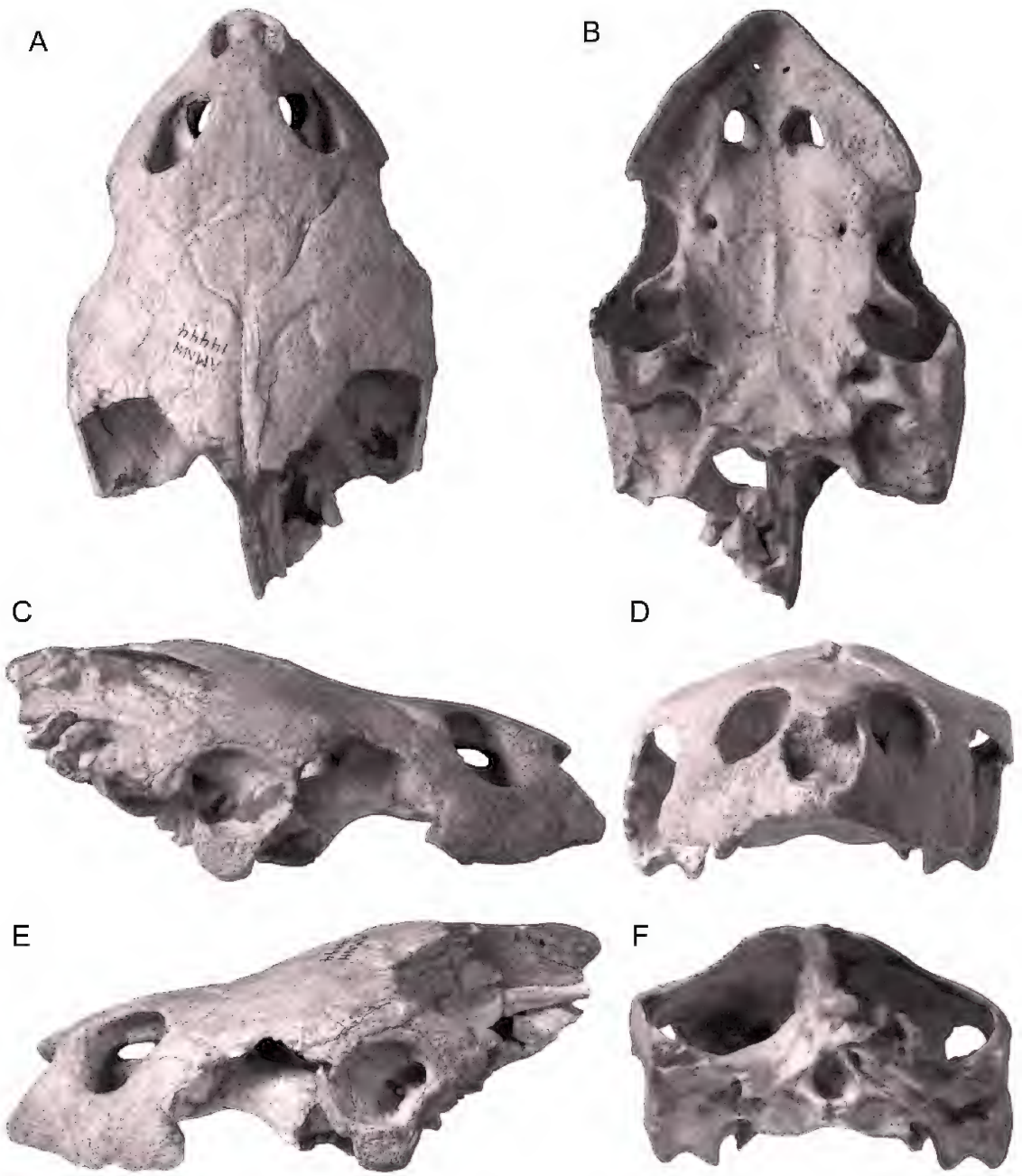



Fig. 21. *Lapparentemys vilavilensis* (Broin, 1971), n. gen. Skull. AMNH 14444 . **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [F. Ippolito, C. Facella, del.]

the postorbital contacts the parietal dorsomedially, the pterygoid ventromedially, and the jugal ventrolaterally. In *Podocnemis* the small postorbital results in a parietal-jugal contact dorsal to the postorbital, a condition absent in *Lapparentemys*, *Peiropemys*, and *Bauruemys*. However, in *Podocnemis* with the postorbital completely retracted from the roof, there is no postorbital exposure on this posterior surface (AMNH 111070).

**Structures of medial process:** As in other pelomedusoides the postorbital in *Lappar-*

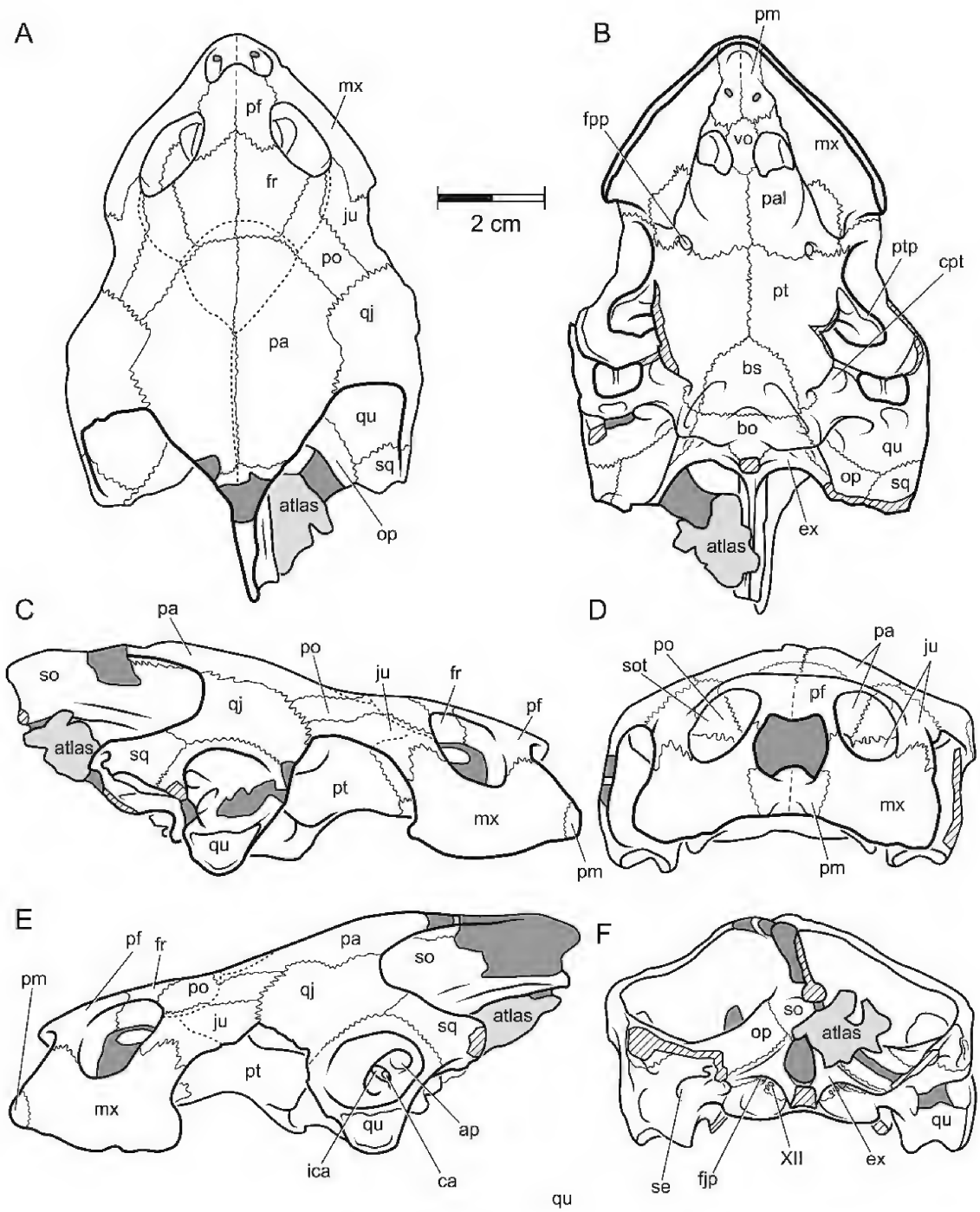



Fig. 22. *Lapparentemys vilavilensis* (Broin, 1971), n. gen. Skull. AMNH 14444. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [F. Ippolito, del.]

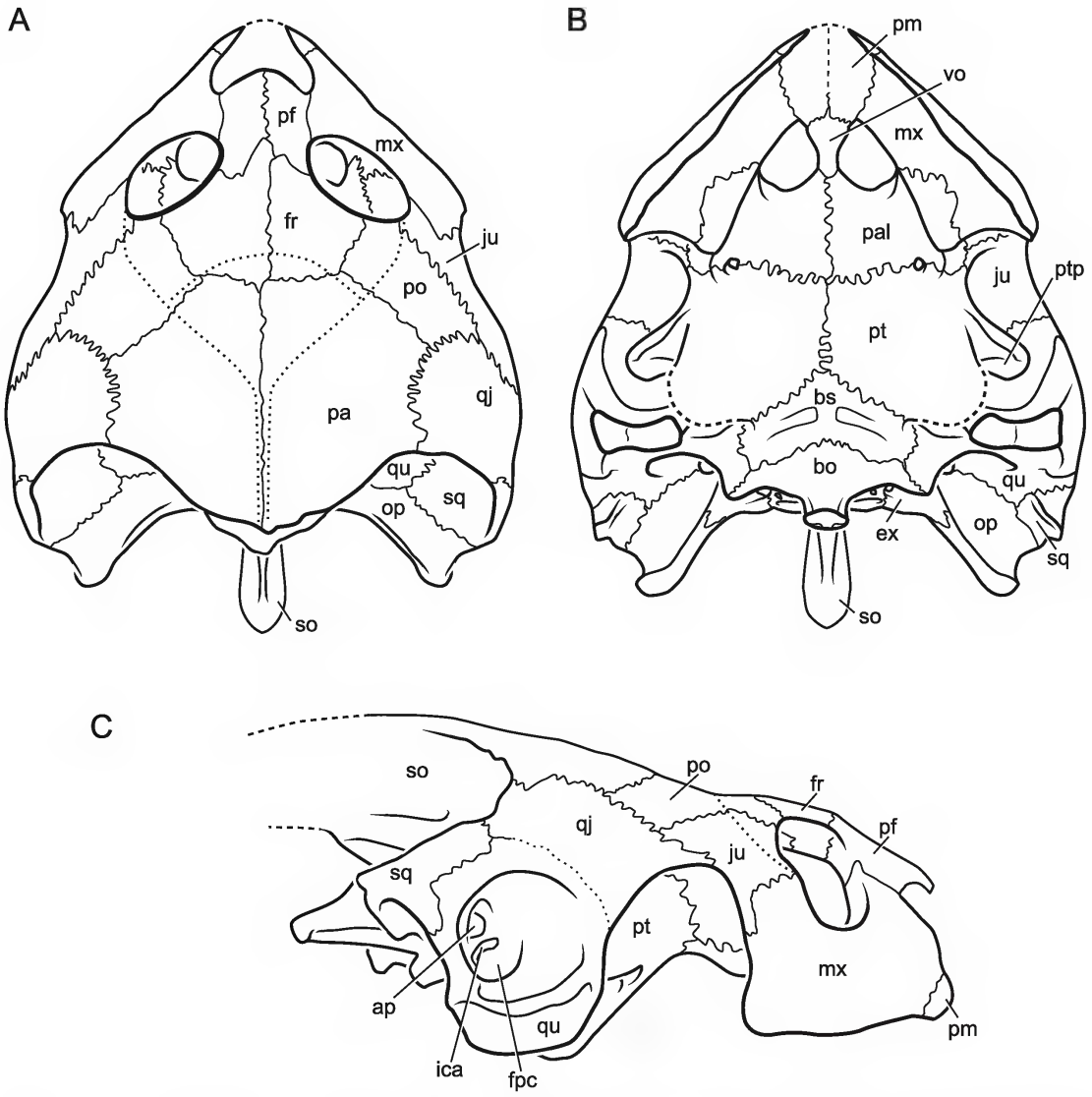



Fig. 23. *Lapparentemys vilavilensis* (Broin, 1971), n. gen. Partially restored skull based on WUS 2160. **A,** dorsal; **B,** ventral; **C,** lateral. [C. Wilson, del.]

*entemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* forms part of the roof and lateral wall of the sulcus palatinopterygoideus and the septum orbitotemporale.

PREMAXILLA (figs. 7, 8, 12, 14, 15, 16, 18, 19, 20, 22, 23, 25)

**Contacts:** The anteromedial part of the premaxilla is missing in *Peiropemys* and completely gone in *Pricemys*, but it is complete in specimens of *Bauruemys* and *Lapparentemys*. In *Lapparentemys*, *Bauruemys*, and *Peiropemys*, the premaxilla contacts the maxilla posterolaterally, the premaxilla medially on the midline, and the vomer posteriorly. In most *Podocnemis* the vomer is absent, so there is no contact, but in *P. vogli* there is what appears to be a vomer (or perhaps a de novo ossification). The anterior palatal area of *Podocnemis* is described in Williams (1954a) and figures repeated in Gaffney (1979: fig. 139).

**Structures on dorsal surface:** The dorsal surface of the premaxilla is visible in speci-

mens of *Lapparentemys*, *Peiropemys*, and *Bauruemys*, and, except for the presence of a well-developed vomer, is very similar to that in *Podocnemis*.

**Structures on ventral surface:** The triturating surface of these podocnemidids provides one of the more useful areas of systematic variation, although, as with most of the rest of the skull, the degree of variation is not great. In *Pricemys* the midline part of the premaxilla is missing, but in *Peiropemys* and *Bauruemys* there is a shallow notch, similar to that seen in *Podocnemis*. There is a shallow midline concavity, similar in depth to that seen in *P. erythrocephala* and *P. expansa,* and not as deep as seen in at least some *P. unifilis* (Williams, 1954a; Gaffney, 1979: fig. 139). In *Lapparentemys* and *Bauruemys* there is no accessory ridge, as in some *Podocnemis* (Gaffney, 1979: fig. 139). Although not complete, it is likely that *Peiropemys* also had a smooth surface right to the midline, as accessory ridges do not usually begin halfway across the premaxilla.

MAXILLA (figs. 7, 8, 12, 14, 15, 16, 18, 19, 20, 22, 23, 25, 26, 27, 31)

**Contacts of vertical plate:** As in pelomedusoides generally, the contacts of the maxilla in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* are with the premaxilla anteromedially, the jugal posterodorsally, and the prefrontal anterodorsally. These contacts are very similar in *Lapparentemys*, *Bauruemys*, *Pricemys,* and *Peiropemys*.

**Structures of vertical plate:** The maxilla forms the ventral part of the orbital margin. The depth of the maxilla is generally greater in *Podocnemis*, *Pricemys,* and *Peiropemys* than it is in *Lapparentemys* and *Bauruemys*, although this difference is slight at best. The foramen orbito-nasale, fossa nasalis, and choanal passages are very similar in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis*. The size and shape of the apertura narium externa is also similar among these taxa, although there seems to be more variation among the species of *Podocnemis* than among *Lapparentemys*, *Bauruemys*, *Pricemys,* and *Peiropemys*.

**Contacts of horizontal plate:** In *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* the maxilla contacts the premaxilla anteromedially, the vomer medially (except in most *Podocnemis* due to the absence of the vomer), the palatine posteromedially, and the jugal posterolaterally. In well-preserved specimens of *Bauruemys* the maxilla sends a narrow process medially to reach the vomer. In the one specimen of *Peiropemys* the maxilla has a broad contact with the vomer and, in a well-preserved specimen of *Lapparentemys* (AMNH 14444), it also has a broad vomer contact. So these taxa are united by a maxilla-vomer contact, but it is narrow in *Bauruemys* and broad in *Peiropemys* and *Lapparentemys*. In *Podocnemis* the possible vomer in *vogli* has a maxilla contact. *Podocnemis expansa* and *P. unifilis* have a broad midline maxilla contact in contrast to the other species.

**Structures of horizontal plate:** All the taxa compared here, *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis,* have relatively narrow triturating surfaces when compared with *Stereogenys* and its close relatives, and the Bothremydini. However, there is some variation among the widths. *Bauruemys* has a skull shape and labial ridge margin that is relatively wider and more obtuse than in *Lapparentemys*, *Peiropemys*, and *Podocnemis*. However, the widths of the triturating surfaces in *Lapparentemys*, *Bauruemys*, *Peiropemys,* and *Pricemys* are very similar, and they all are narrower anteriorly, widening posteriorly. The surfaces themselves have a slight increase in height along the margin of the apertura narium interna, and a slight concavity posteriorly, at the widest part of the triturating surface. The species of *Podocnemis* vary much more; all have some type of accessory ridge or ridges (Williams, 1954a; Gaffney, 1979: fig. 139), absent in *Lapparentemys*, *Bauruemys*, *Pricemys,* and *Peiropemys*.

The palatine forms the posteromedial part of the triturating surface in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis*, although there is more variation in the degree of this contribution among the species of *Podocnemis* than among the specimens of *Lapparentemys*, *Pricemys, Peiropemys*, and *Bauruemys*. The apertura narium interna is formed laterally by the maxilla and it is similar among the four taxa. In *Peirop-*

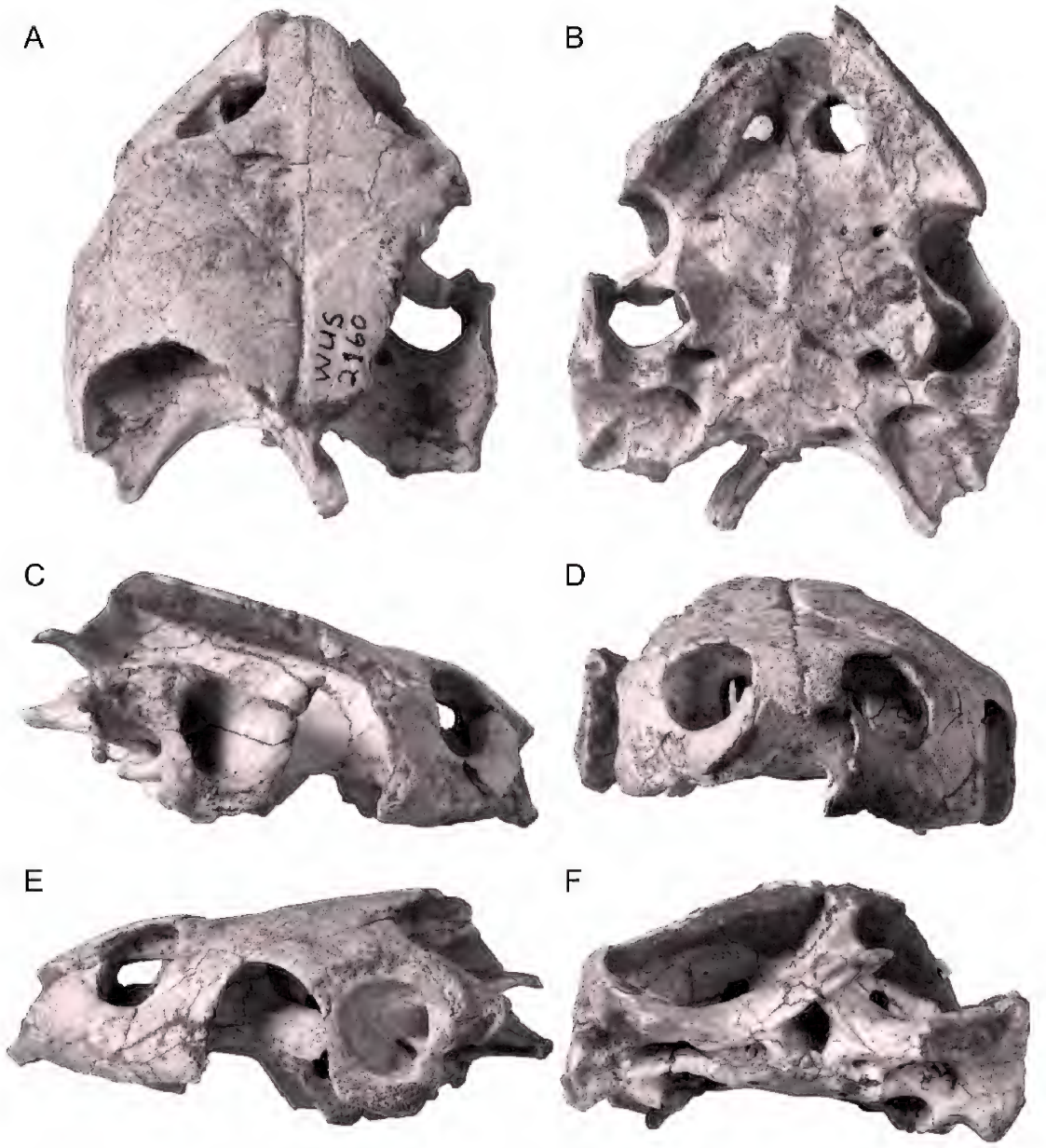



Fig. 24. *Lapparentemys vilavilensis* (Broin, 1971), n. gen. Skull WUS 2160. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [F. Ippolito, C. Facella, del.]

*emys* the maxilla forms a slightly narrower margin laterally than in *Pricemys*, *Bauruemys* and *Lapparentemys*. In *Podocnemis*, however, the apertura varies more in shape and width (Williams, 1954a; Gaffney, 1979: fig. 139). In addition to being wider, the triturating surface of *Pricemys* differs from that in *Peiropemys* in having a shallow concavity posterolaterally.

VOMER (figs. 7, 8, 12, 14, 15, 16, 18, 19, 20, 22, 23, 24)

**Contacts:** As in other pelomedusoides the vomer contacts in *Lapparentemys*, *Peiropemys*, and *Bauruemys* are with the premaxillae anteriorly, the maxillae anterolaterally, and the palatines posteriorly. *Pricemys* has the area of the vomer missing. In *Podocnemis*

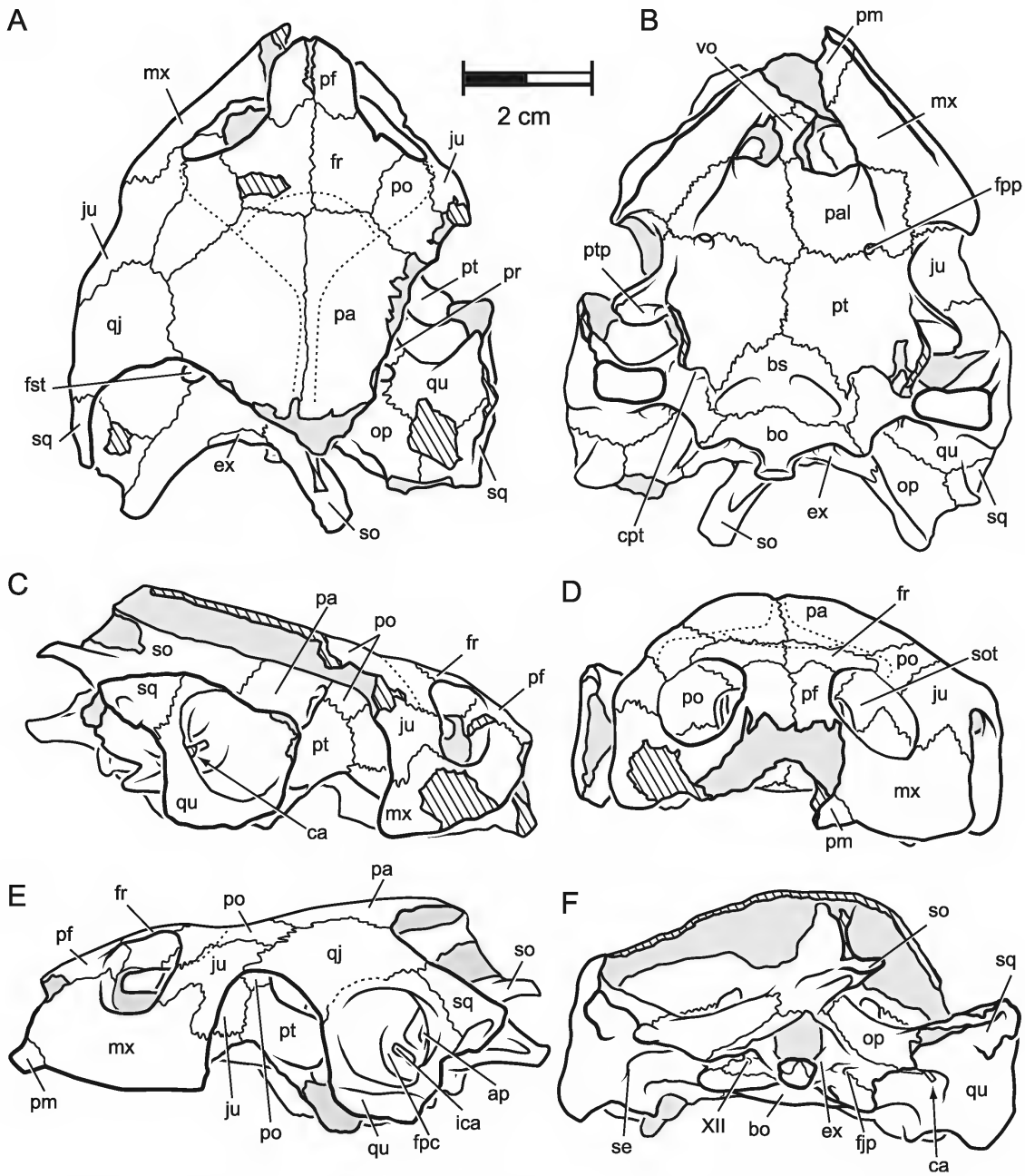



Fig. 25. *Lapparentemys vilavilensis* (Broin, 1971), n. gen. Skull WUS 2160. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [C. Wilson, del.]

the vomer is absent, except in *P. vogli*. Examination of specimens of *vogli* and the other species of *Podocnemis*, suggests that the supposed vomer in *vogli* might be a neomorph formed from the anterior end of one of the palatines. This "vomer" lacks the characteristic contacts and shape, and is very small, sometimes just embedded in the connective tissue forming the internarial bar.

**Structures:** The vomer in *Lapparentemys*, *Peiropemys*, and *Bauruemys* is the usual dumbbell-shaped, relatively thick, columnar

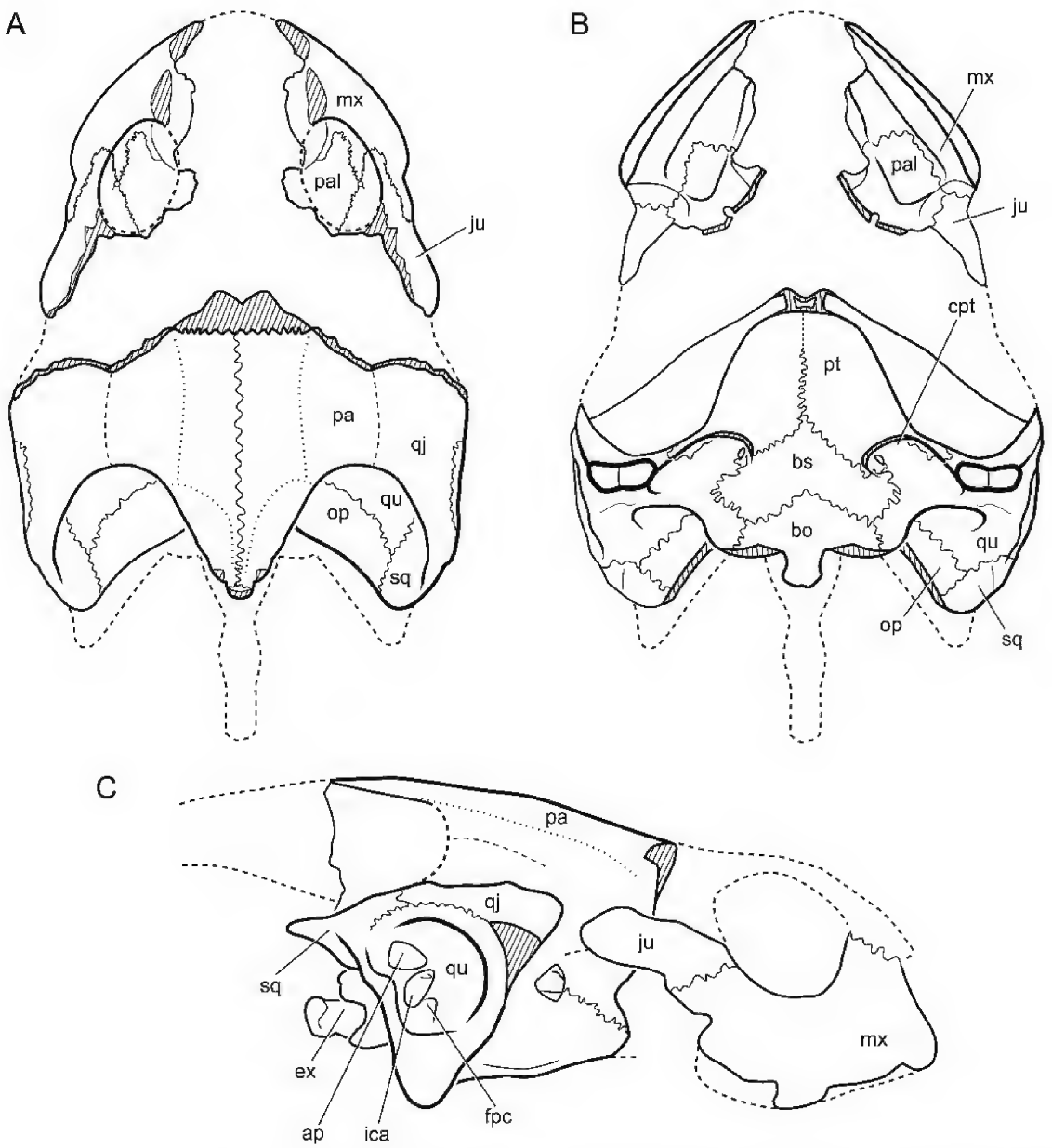



Fig. 26. *Pricemys caiera,* n. gen. et sp. Partially restored skull based on DGM MCT 1498-R. **A,** dorsal; **B,** ventral; **C,** lateral. [M. Beveridge, del.]

bone, separating the choanal passages of the apertura narium interna with no development of a secondary palate.

PALATINE (figs. 7, 8, 12, 14, 15, 16, 18, 19, 20, 22, 23, 25, 26, 27, 31)

**Contacts:** In *Lapparentemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis,* there are the usual pelomedusoides contacts of the palatine with the maxilla anterolaterally, the vomer anteromedially, the other palatine medially on midline, and the pterygoid posteriorly. Only the lateral part of the palatine is present in *Pricemys*. On the dorsal surface there is a small contact with the parietal (processus inferior parietalis).

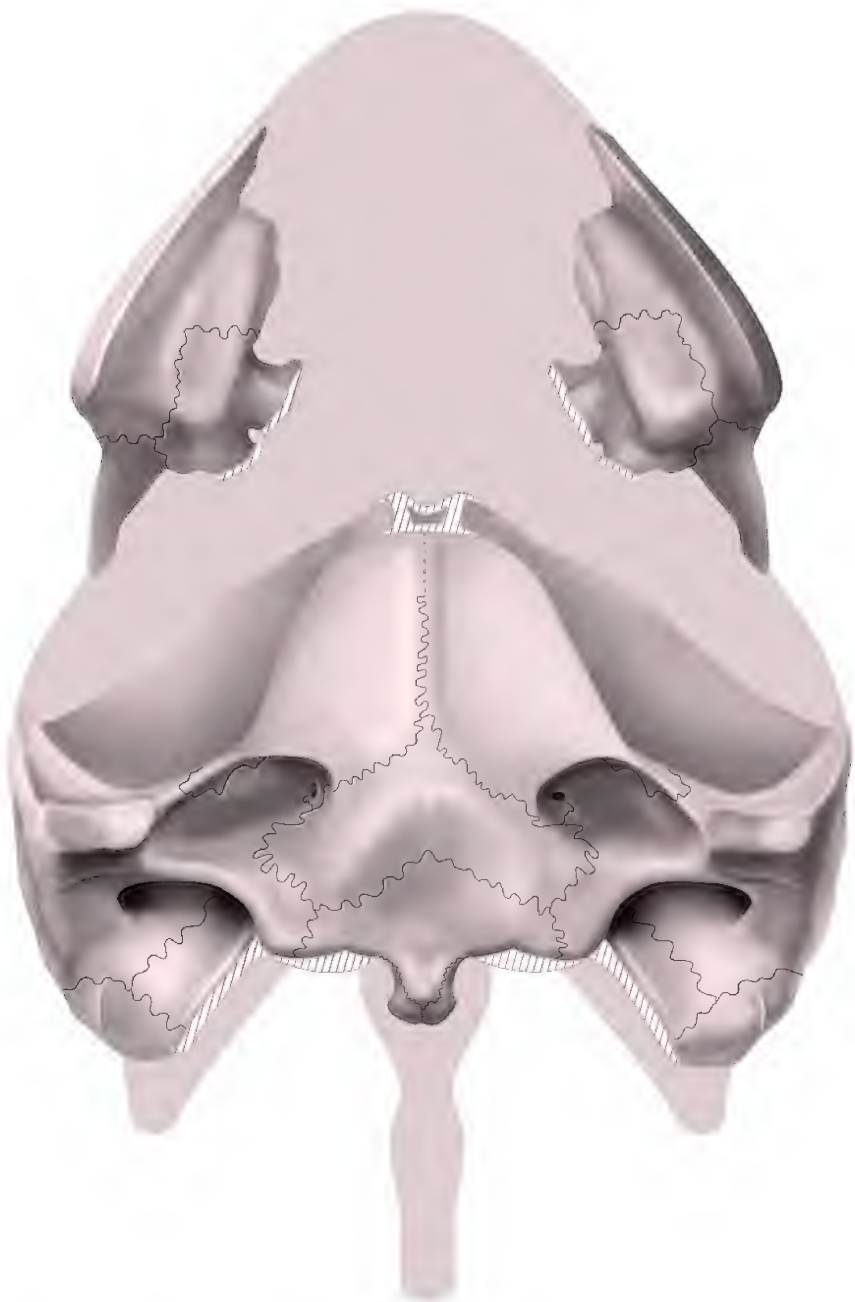


Fig. 27. *Pricemys caiera,* n. gen. et sp. Partially restored ventral view of skull based on DGM MCT 1498-R. [M. Beveridge, del.]

In the floor of the fossa orbitalis in *Lapparentemys* and *Peiropemys* the contacts are with the maxilla anterolaterally, the jugal laterally, and the postorbital posterolaterally. This is the case on the right side of one *Bauruemys* (MCZ 4123), but on its left side the maxilla contacts the postorbital and separates the palatine-jugal contact. In the other *Bauruemys* specimens the area is unclear.

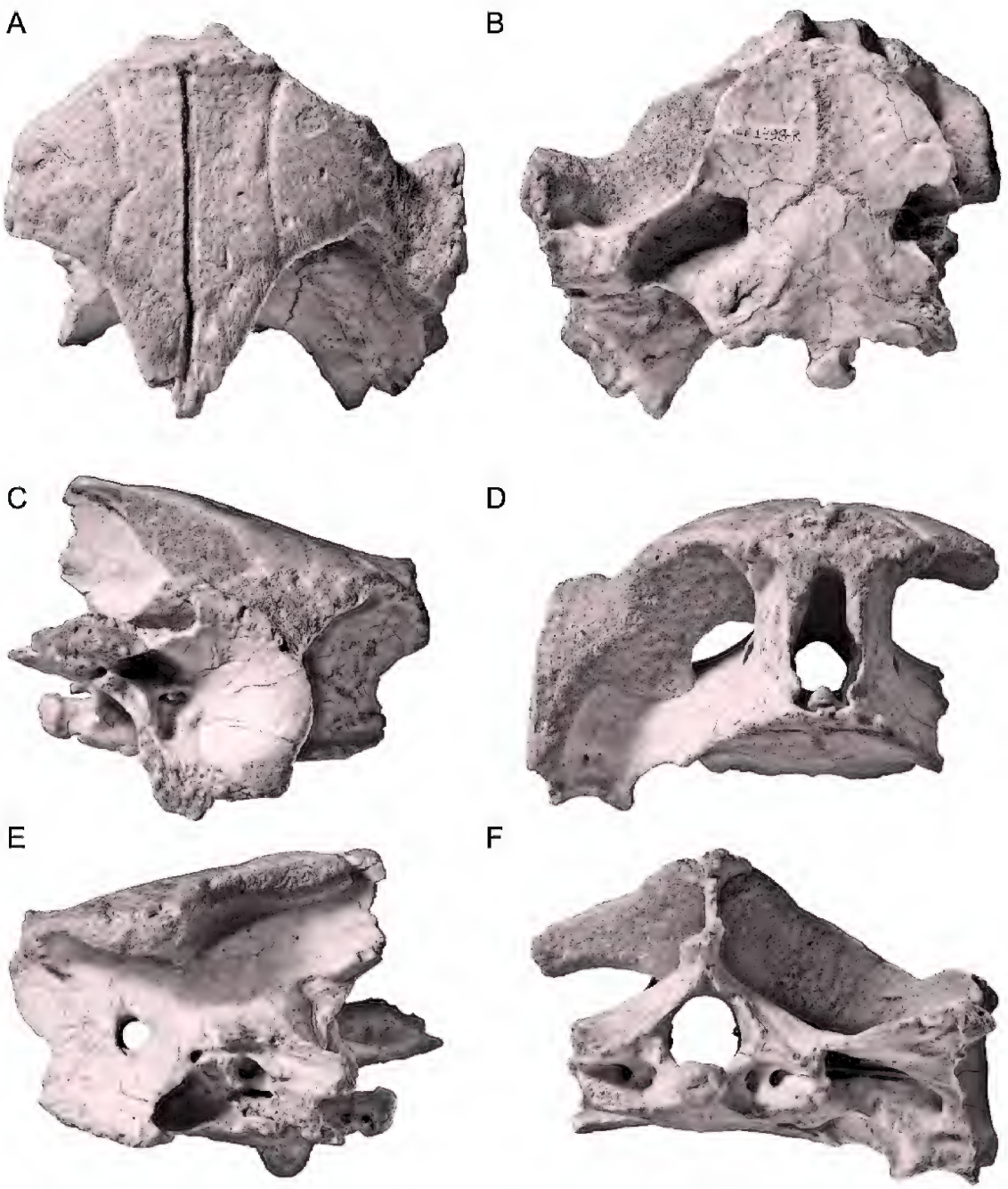



Fig. 28. *Pricemys caiera,* n. gen. et sp. DGM MCT 1498-R. Braincase moiety. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [C. Facella, del.]

**Structures:** The palatine is very similar in *Lapparentemys*, *Peiropemys*, and *Bauruemys*. In *Podocnemis* there is a low but acute ridge partially separating the fossa nasalis from the more ventral choanal passage. This shelf is less developed in *Lapparentemys*, *Peiropemys*, and *Bauruemys*. The palatine forms the posteromedial part of the triturating

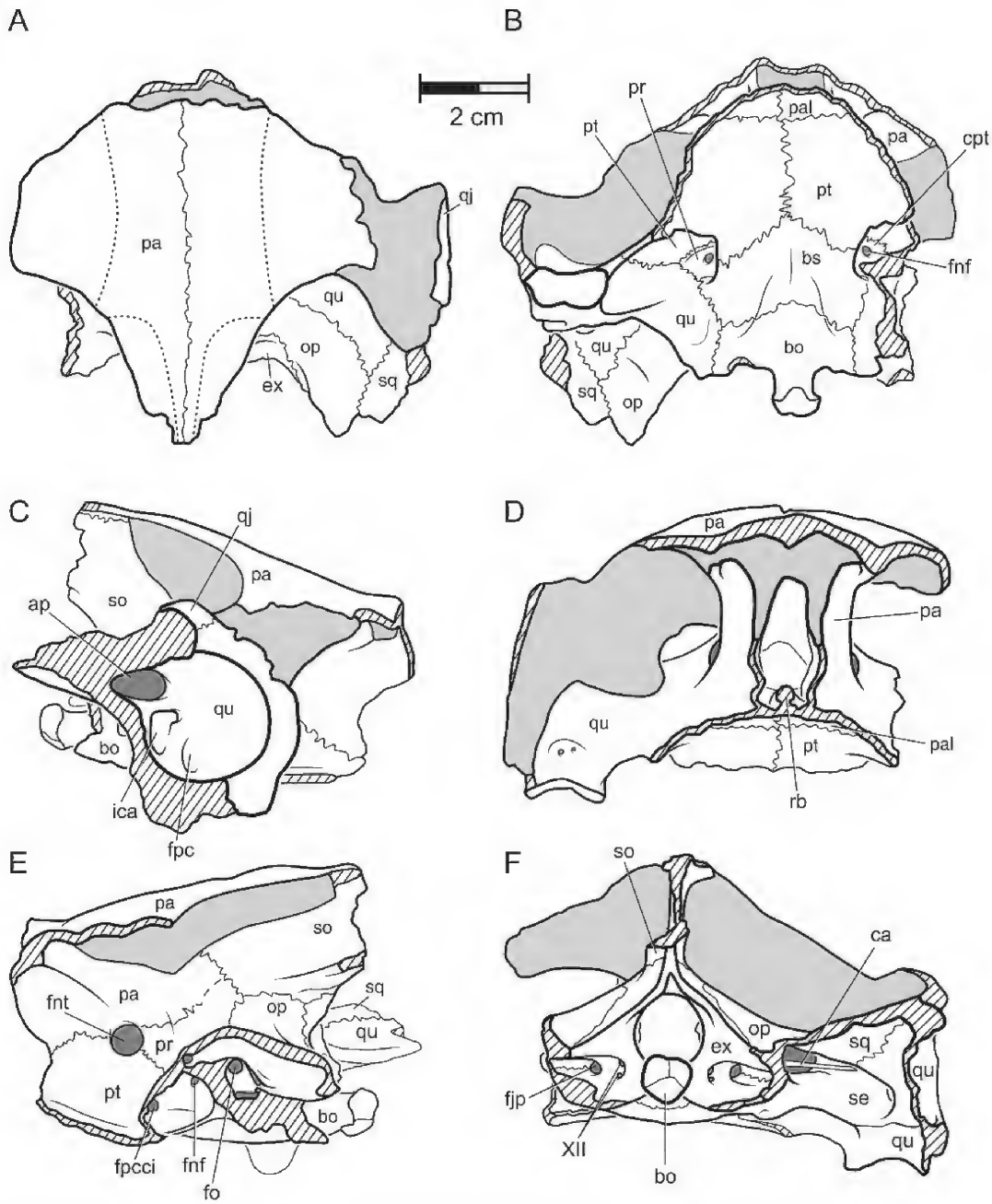



Fig. 29. *Pricemys caiera,* n. gen. et sp. DGM MCT 1498-R. Braincase moiety. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [C. Facella, del.]

surface in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis*, but its contribution is much more variable in *Podocnemis.* The apertura narium interna lies open on the palate in *Lapparentemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis*, without any constrictions or deep choanal grooves marking it.

The foramen palatinum posterius is formed between the palatine and pterygoid

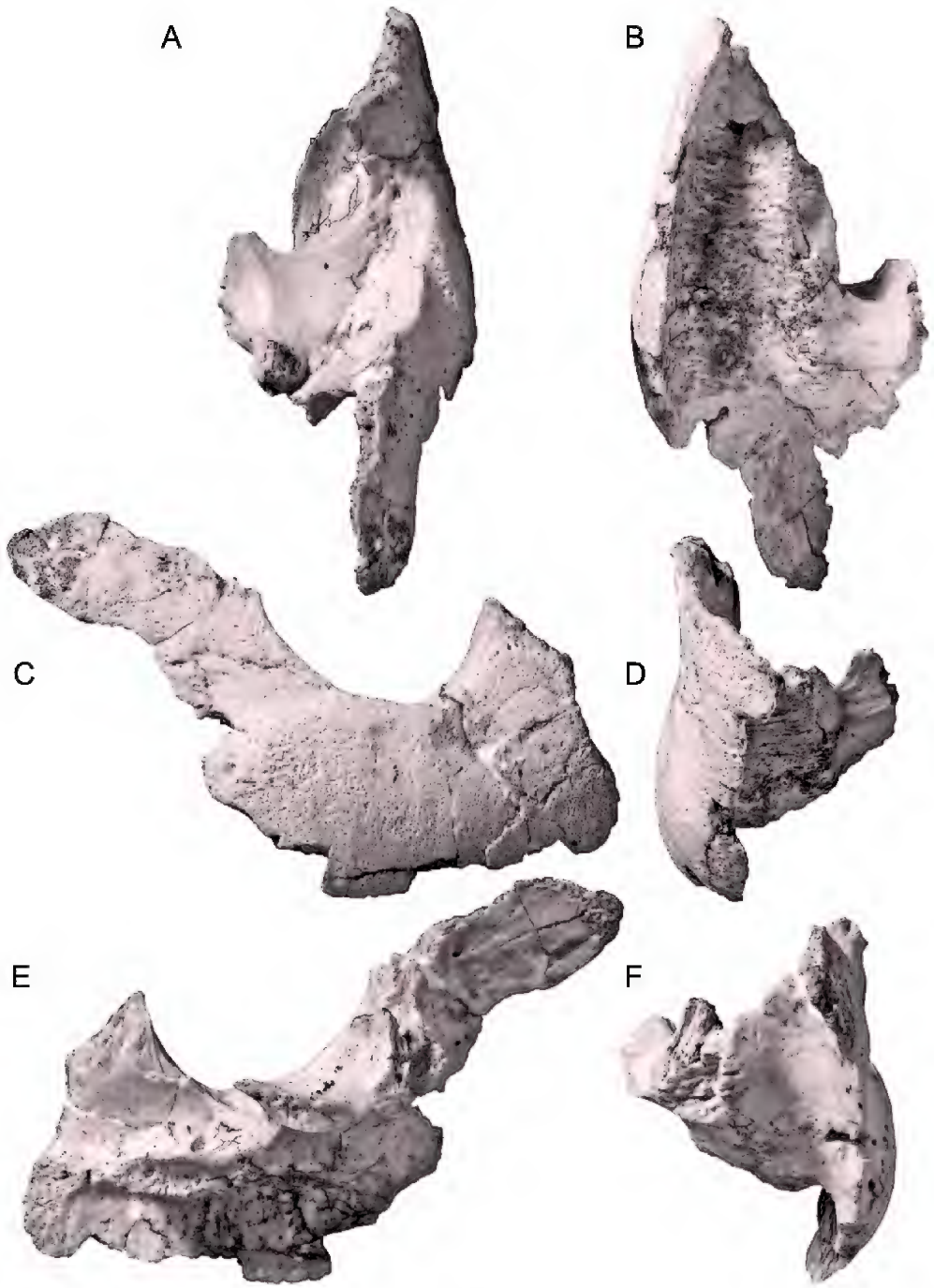



Fig. 30. *Pricemys caiera,* n. gen. et sp. DGM MCT 1498-R. Jugal-maxilla-palatine moiety. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [C. Facella, del.]

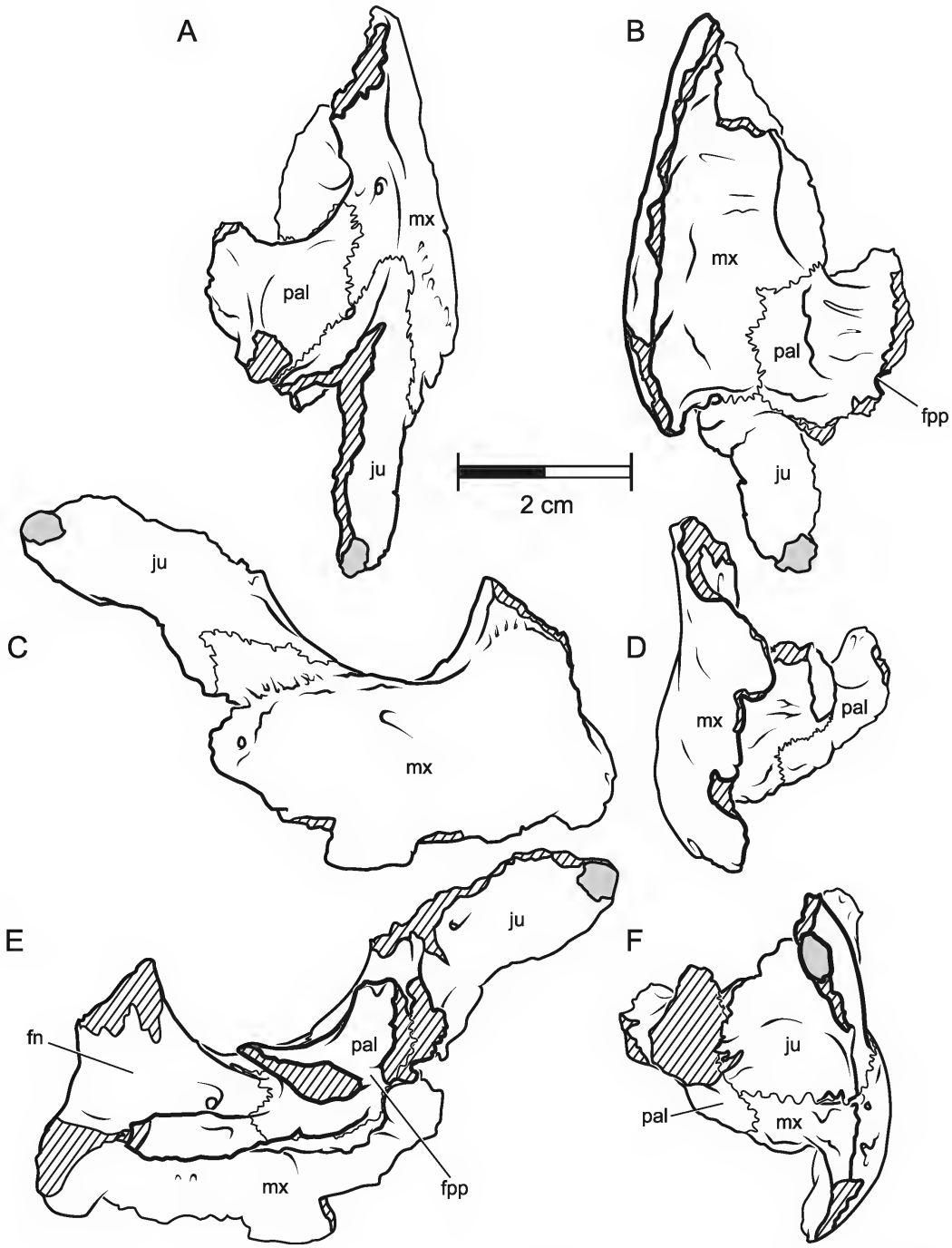



Fig. 31. *Pricemys caiera,* n. gen. et sp. DGM MCT 1498-R. Jugal-maxilla-palatine moiety. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [J. Sharkey, del.]

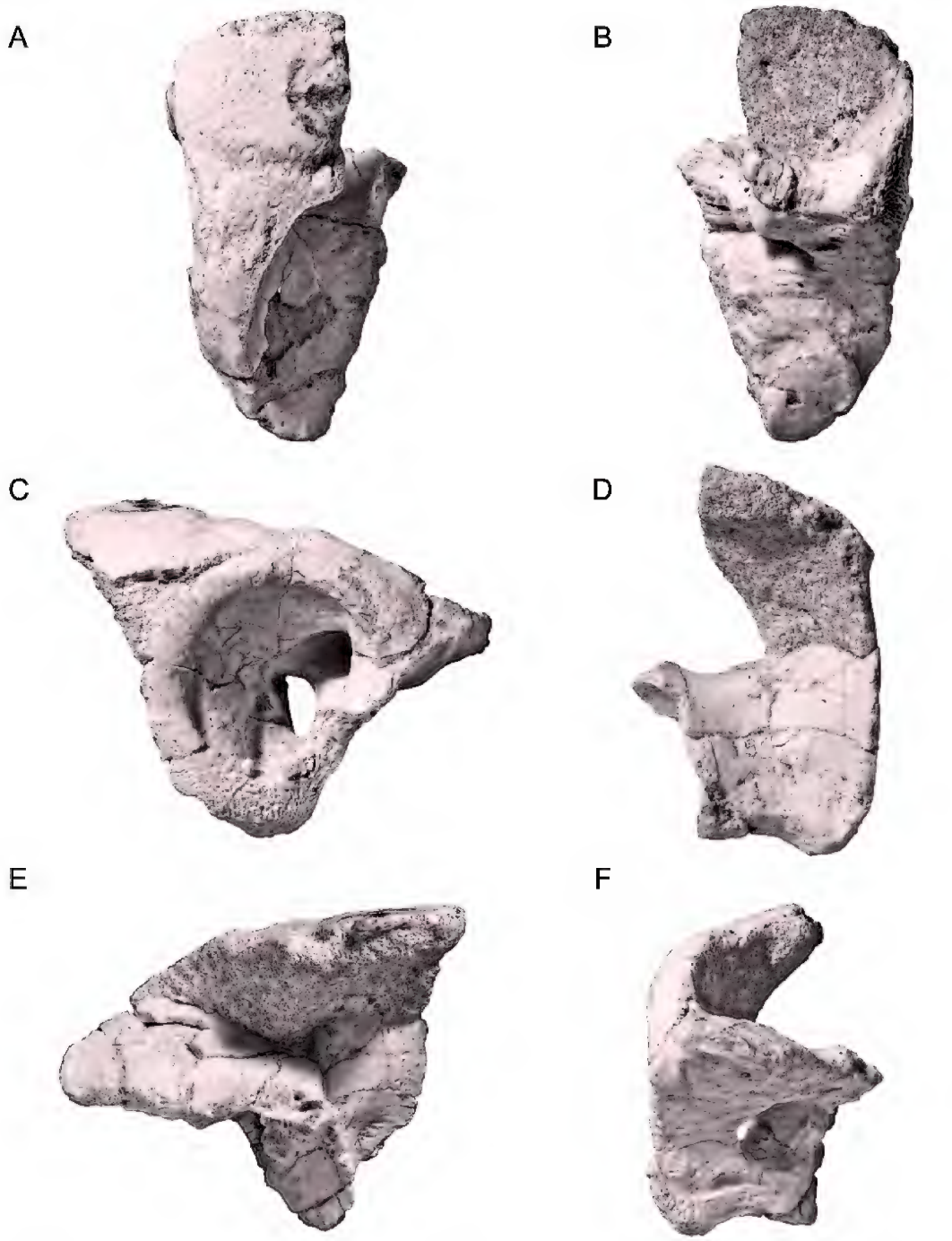



Fig. 32. *Pricemys caiera,* n. gen. et sp. DGM MCT 1498-R. Left quadrate moiety. **A,** dorsal; **B,** ventral; **C,** left lateral; **D,** anterior; **E,** medial; **F,** posterior. [C. Facella, del.]

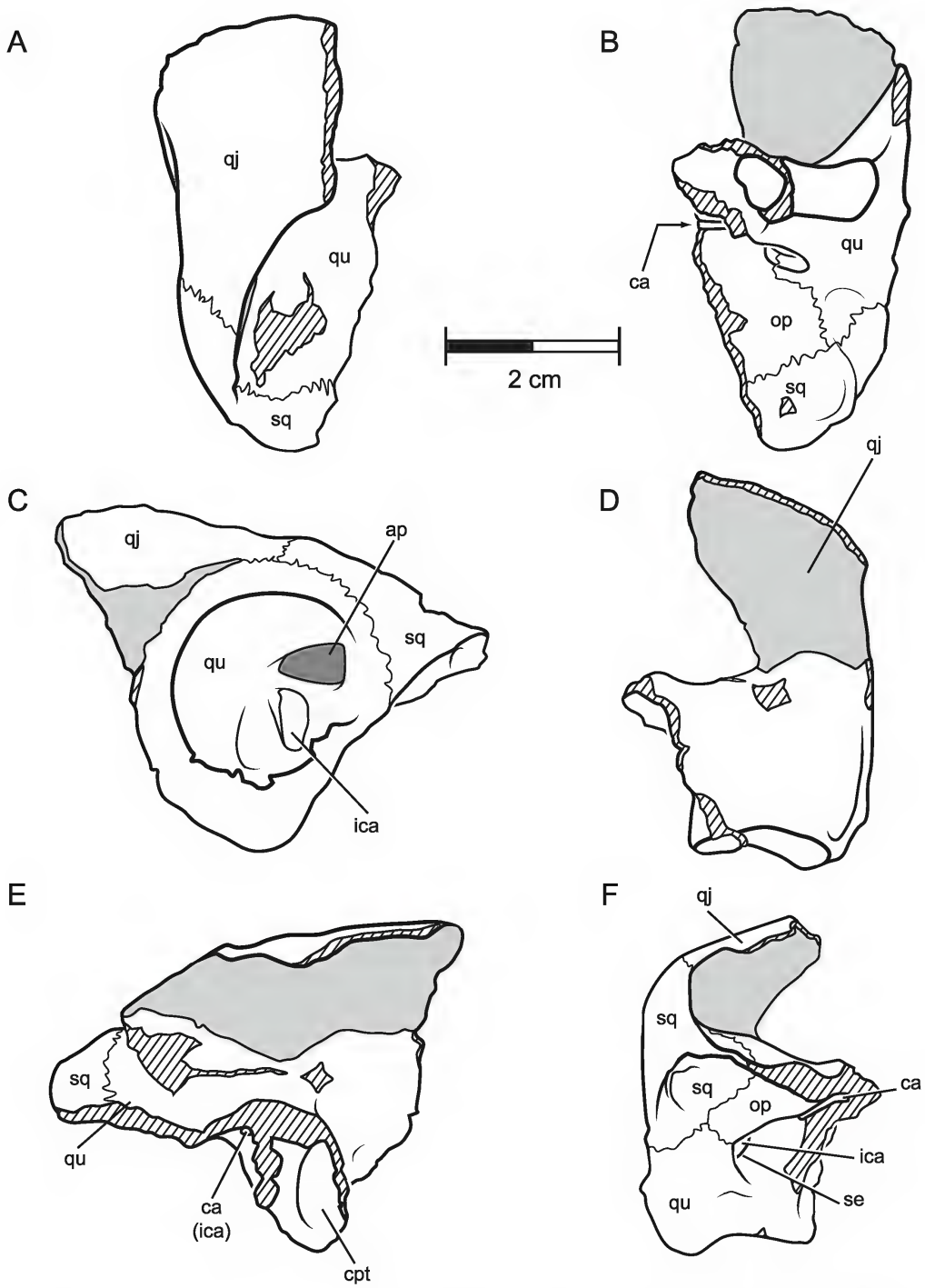



Fig. 33. *Pricemys caiera,* n. gen. et sp. DGM MCT 1498-R. Left quadrate moiety. **A,** dorsal; **B,** ventral; **C,** left lateral; **D,** anterior; **E,** medial; **F,** posterior. [C. Facella, del.]

Fig. 34. ?*Pricemys caiera,* n. gen. et sp. DGM MCT ? R. Dorsal view of lower jaw, right ramus reversed. [F. Ippolito, del.]

bones laterally, close to the triturating surface. It is similar in position in *Lapparentemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis.* It is formed almost entirely by the palatine in these taxa.

QUADRATE (figs. 7, 8, 12, 14, 15, 16, 18, 19, 20, 22, 23, 25, 26, 27, 31, 33)

**Contacts on lateral surface:** The quadrate in *Lapparentemys*, *Peiropemys*, *Bauruemys*, *Pricemys*, and *Podocnemis* contacts the quadratojugal anterodorsally, and the squamosal posterodorsally. The quadratojugal-quadrate contact is preserved in the left quadrate moiety in *Pricemys* (fig. 33). Despite some variation in the degree of temporal emargination, these contacts are all similar in these taxa.

**Structures on lateral surface:** The quadrate in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* does not enter the temporal margin due to the quadratojugal-squamosal contact found in all. The cavum tympani structures usually show significant variation among turtles, but in these taxa, the variation is mostly among the *Podocnemis* species. In *Lapparentemys*, *Pricemys*, *Peiropemys*, and *Bauruemys* the incisura columellae auris is closed by the quadrate forming a broad wall. The incisura itself includes the eustachian tube, in contrast to bothremydids. The incisura in *Lapparentemys, Bauruemys*, *Pricemys,* and *Peiropemys* is similar to that structure in *Podocnemis*, but relatively smaller in size.

The antrum postoticum in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* is similar in size and shape. The antrum in *Peiropemys* is slightly higher and more circular than in the flatter ones seen in *Lapparentemys* and *Bauruemys*. The antrum is slightly larger in *Peiropemys* than in *Pricemys*. The size of the opening varies slightly among the *Lapparentemys*, *Bauruemys*, *Peiropemys,* and *Pricemys,* but all of them are close in size to that seen in *Podocnemis expansa.* This antrum size is larger than that seen in *Kurmademys* and

Pelomedusidae, but only slightly smaller than the antrum of *Euraxemys*.

A fossa precolumellaris is present in *Lapparentemys*, *Pricemys*, *Peiropemys*, and *Bauruemys*, just anterior to the incisura columellae auris, as in *Podocnemis*. In *Peiropemys* and *Bauruemys* (AMNH 7888) the fossa is small but deep, while in *Lapparentemys* and *Pricemys* it is wide and shallow. The fossa seen in *Peiropemys* and *Bauruemys* agrees most closely with that in *Podocnemis unifilis* (AMNH 58199). In the genus *Podocnemis* the fossa shows variation used by Williams (1954a) to help distinguish species. Although there is individual variation, *P. unifilis* and *P. expansa* show a shallow fossa precolumellaris while the other species have deeper ones.

Both the antrum postoticum size and the fossa precolumellaris size are continuous variables that are hard to quantify and must be subjectively divided into comparable states. Some authors may adopt present or absent while others try for more subtle distinctions. We use states that seem reasonable to us with the material available to us.

**Contacts on dorsal and anterior surface:** As is the usual case for pelomedusoides the contacts in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* are with the prootic anteromedially, the opisthotic posteromedially, and the squamosal posteriorly and posterolaterally.

**Structures on dorsal and anterior surface:** The foramen stapedio-temporale is formed between the quadrate and prootic as is the case in generalized pelomedusoides. Its position is the same in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis*.

**Contacts on ventral surface:** In *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* and generalized pelomedusoides the contacts are with the pterygoid anteromedially, the basisphenoid medially, the basioccipital posteromedially, and the prootic medially.

**Structures on ventral surface:** A diagnostic feature of the Podocnemididae is the cavum pterygoidei, which is roofed in part by the quadrate. As other elements make up most of the cavity, the cavum pterygoidei, and the related foramen posterius canalis carotici interni, are described elsewhere (see Pterygoid). The position of the condylus mandibularis relative to the condylus occipitalis is about the same in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis*.

**Contacts on posterior surface:** As in more generalized pelomedusoides, the contacts are with the squamosal dorsolaterally, the opisthotic dorsomedially, the exoccipital medially, the basioccipital ventromedially, and the prootic ventromedially. The prootic contact in podocnemidids is covered ventrally by the pterygoid in the cavum pterygoidei.

**Structures on posterior surface:** The fenestra postotica in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* has only shallow ridge subdivisions for the lateral head vein and stapedial artery, not complete foramina as in some bothremydids. The posterior of the quadrate is open in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* with the sulcus eustachii, incisura columellae auris, and stapes visible in posterior view. The foramen chorda tympani inferius is in about the same position in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis*; on the posterior surface of the processus articularis, just below the incisura columellae auris.

PTERYGOID (figs. 7, 8, 12, 14, 15, 16, 18, 19, 20, 22, 23, 25, 26, 27, 29)

**Contacts on ventral surface:** In *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* the contacts are with the palatine anteriorly, the other pterygoid anteromedially, and the basisphenoid posteromedially. Within the cavum pterygoidei the pterygoid also contacts the prootic posteriorly, the quadrate posterolaterally, and the basisphenoid.

**Structures on ventral surface:** The processus trochlearis pterygoidei in *Lapparentemys*, *Peiropemys, Bauruemys*, and *Podocnemis* (not preserved in *Pricemys*) is large and extends laterally into the fossa temporalis. In *Podocnemis* the process lies at nearly a right angle to the midline. In *Lapparentemys* and *Peiropemys* it is slightly less than a right angle, and in *Bauruemys* it is at less of an angle than in *Lapparentemys* and *Peiropemys*. However, these are subjective assessments: measurements show these angles to be

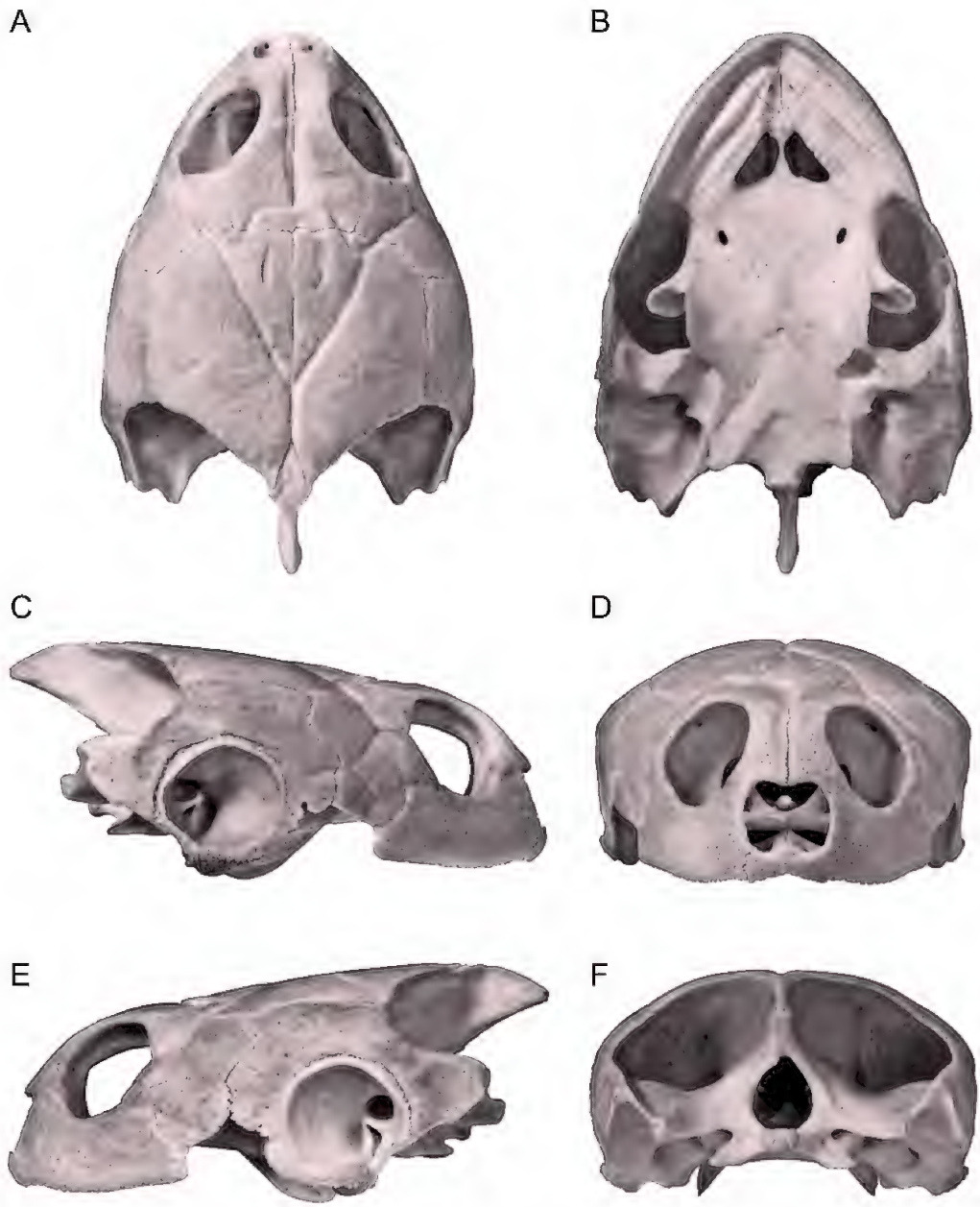



Fig. 35. *Podocnemis vogli* Müller, 1935. Skull, UF 39100. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [M. Vabulas, del.]

very close and within the variations caused by different observers.

The cavum pterygoidei (for contents, see Character Discussion below and Albrecht, 1976; Gaffney, 1979; Schumacher, 1954, 1955a, 1955b, 1956, 1973) is formed by four bones: the basisphenoid anteriorly and medially, the pterygoid ventrally and laterally, the prootic posterodorsally, and the quadrate posterodorsolaterally. There are five foramina in the cavum pterygoidei in *Pricemys* and *Peiropemys*. Posteromedially along the length of the basisphenoid is the foramen nervi abducentis (1). More anteri-

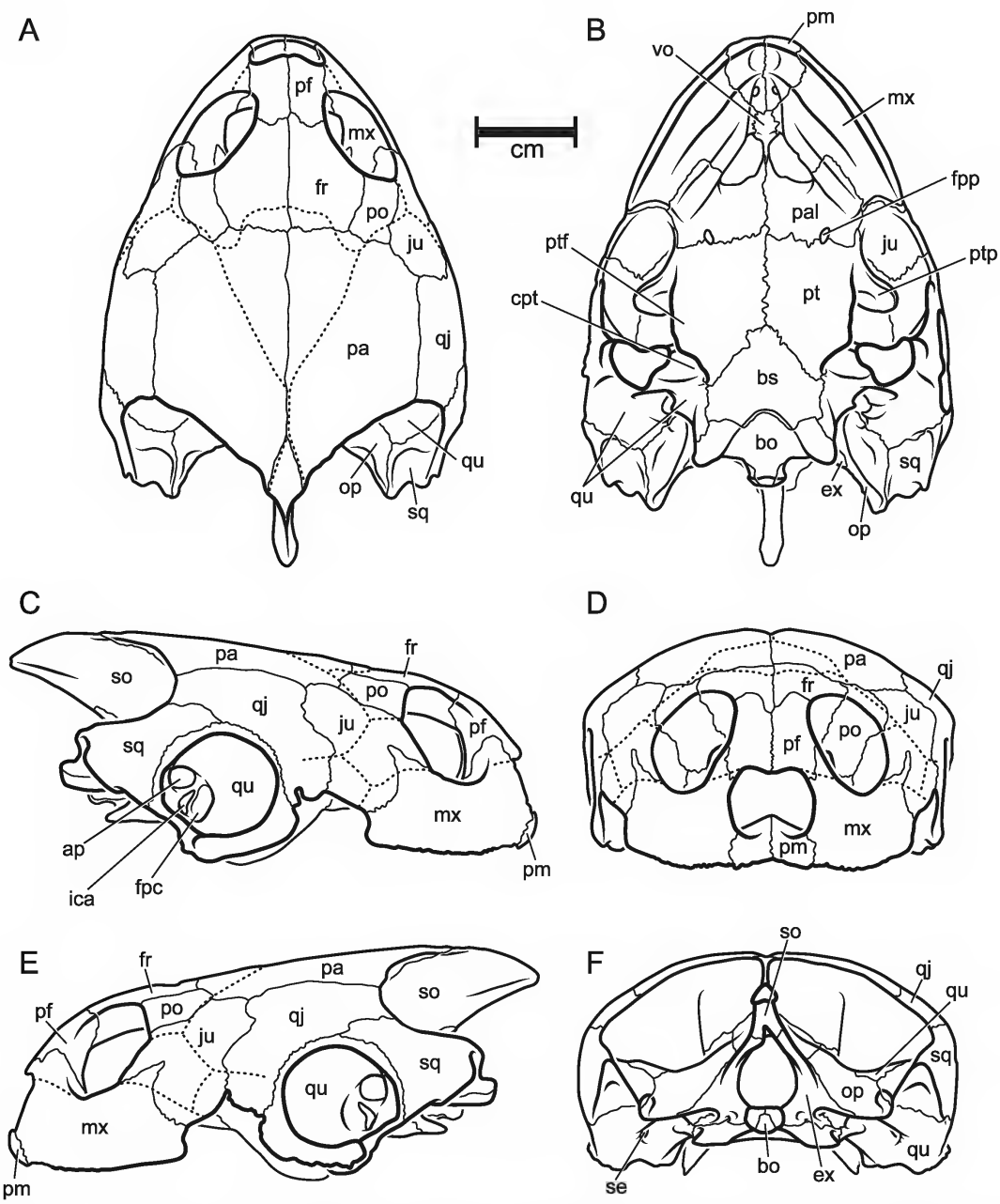



Fig. 36. *Podocnemis vogli* Müller, 1935. Skull, UF 39100. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [M. Vabulas, del.]

orly, also within the basisphenoid, near the anterior limit of the cavum pterygoidei is the foramen posterius canalis carotici interni (2); just lateral to this is the foramen caroticum laterale (3). The pterygoid-basisphenoid suture is lateral to the foramen caroticum laterale, and lateral to that contact and within the pterygoid, is the foramen nervi vidiani (4). More posteriorly in the cavum, in its dorsal surface, the prootic is exposed. The foramen nervi facialis (5) lies in the center of the prootic. These foramina can be probed in the braincase of *Pricemys* (fig. 27), which has had nearly all the matrix removed in the

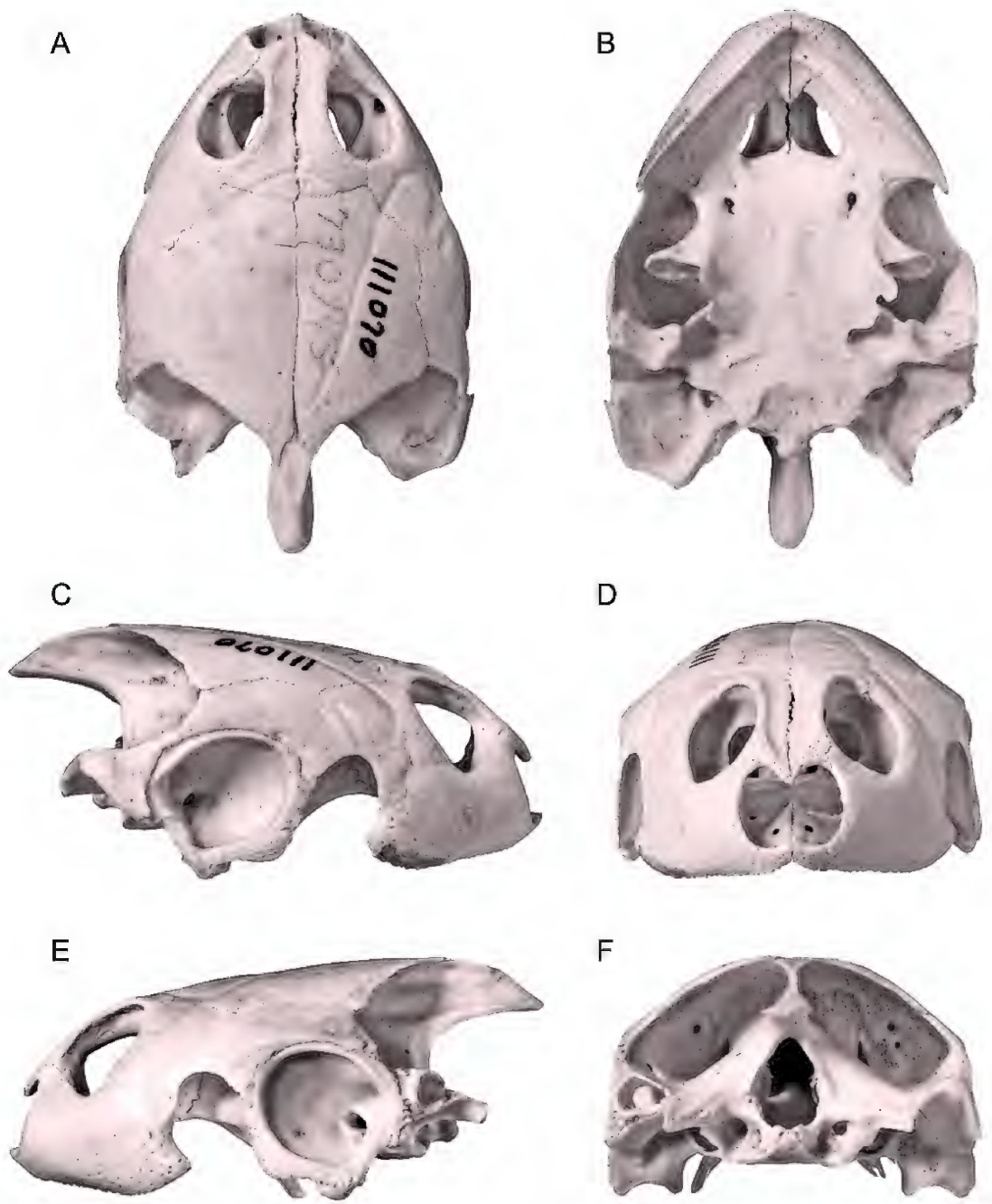



Fig. 37. *Podocnemis sextuberculata* Cornalia, 1849. Skull, AMNH 111070 **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [M. Vabulas, del.]

cavum cranii and both cava pterygoidei. *Bauruemys,* MCT 1753-R (figs. 11, 12), has the cavum pterygoidei exposed on both sides. Here the foramen posterius canalis carotici interni appears to be combined with the foramen caroticum laterale as one oval opening, possibly damaged by preservation. So this specimen has four foramina comparable in position to those in *Pricemys* and *Peiropemys*. Unfortunately, none of the

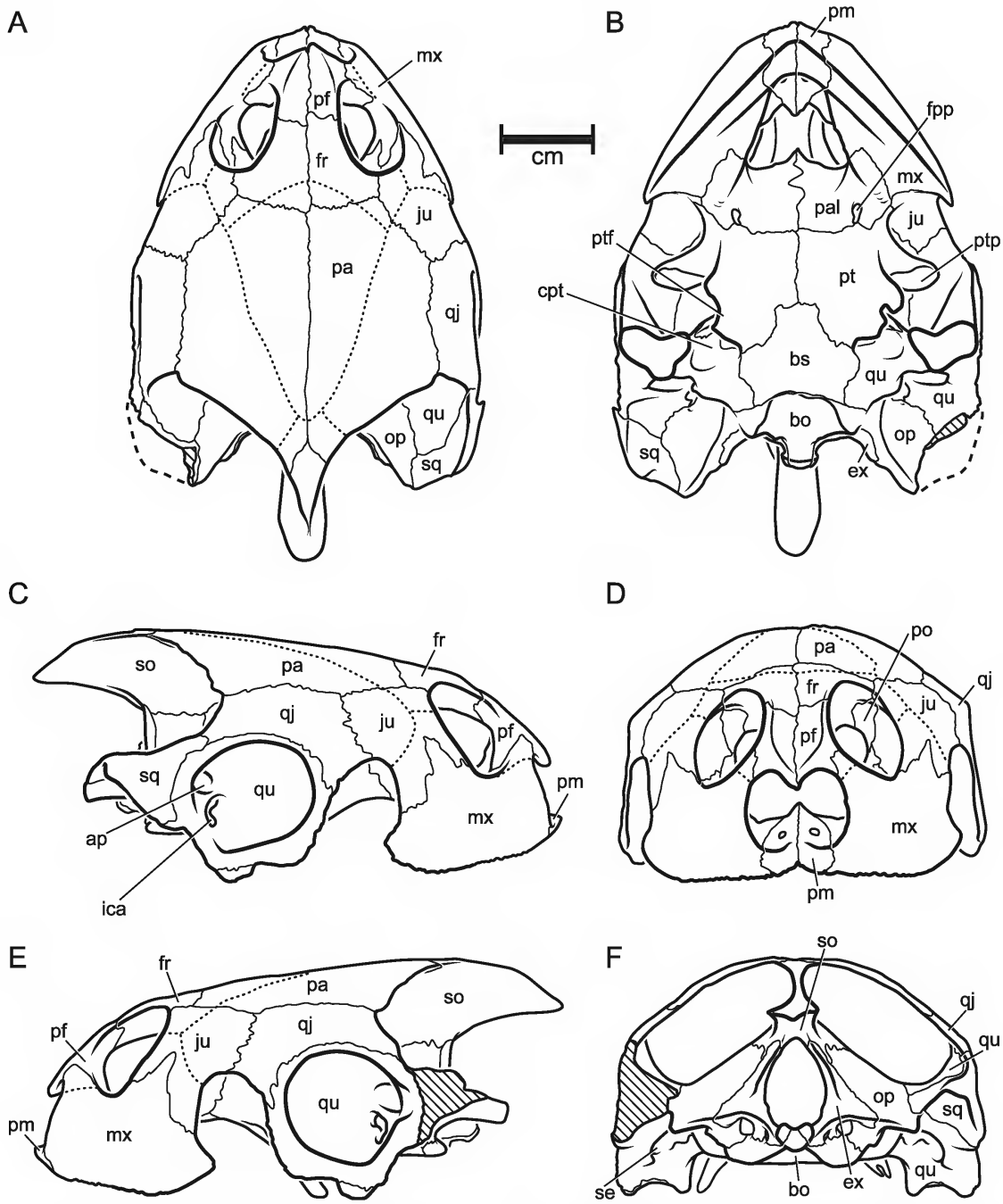



Fig. 38. *Podocnemis sextuberculata* Cornalia, 1849. Skull, AMNH 111070 **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [M. Vabulas, del.]

*Lapparentemys* specimens are as well preserved or as matrix-free as the *Pricemys* and *Peiropemys*, but the areas preserved agree with the *Pricemys* and *Peiropemys* morphology. The skull figured in Broin (1991: pl. 2, figs. 1–7, "Tiupampa"), which is presumably *Lapparentemys vilavilensis* (it is possible that other taxa are figured as well, see discussion

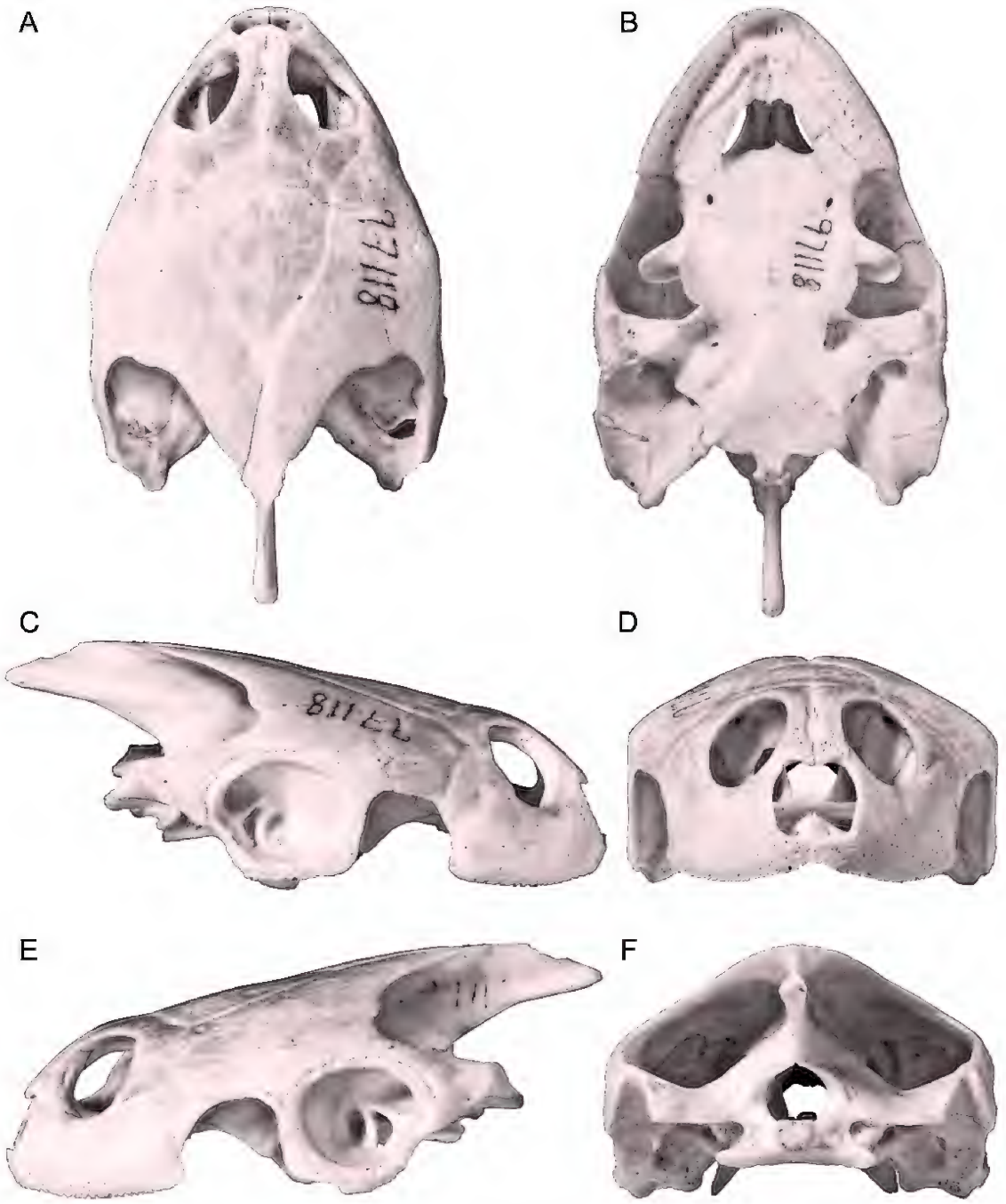



Fig. 39. *Podocnemis unifilis* Troschel, 1848. Skull, AMNH 97118. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [C. Facella, del.]

under *L. vilavilensis*), has nearly all of the cavum preserved on one side or the other, and it has the *Pricemys* and *Peiropemys* condition.

The pterygoid flange is broken in *Pricemys*, *Peiropemys*, and *Lapparentemys*, most specimens of *Bauruemys*, and frequently in recent *Podocnemis* as well, because it is so

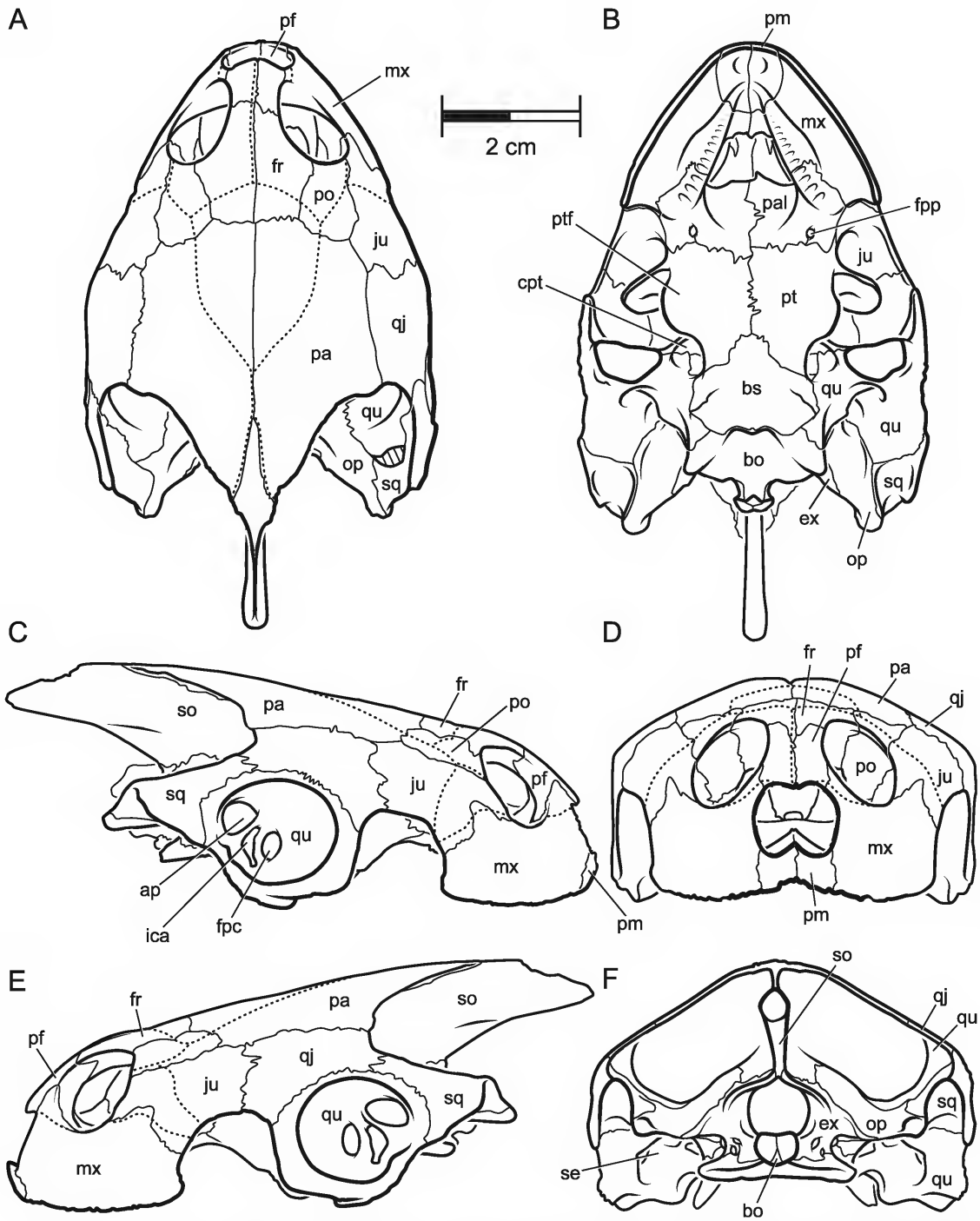



Fig. 40. *Podocnemis unifilis* Troschel, 1848. Skull, AMNH 97118. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [C. Facella, del.]

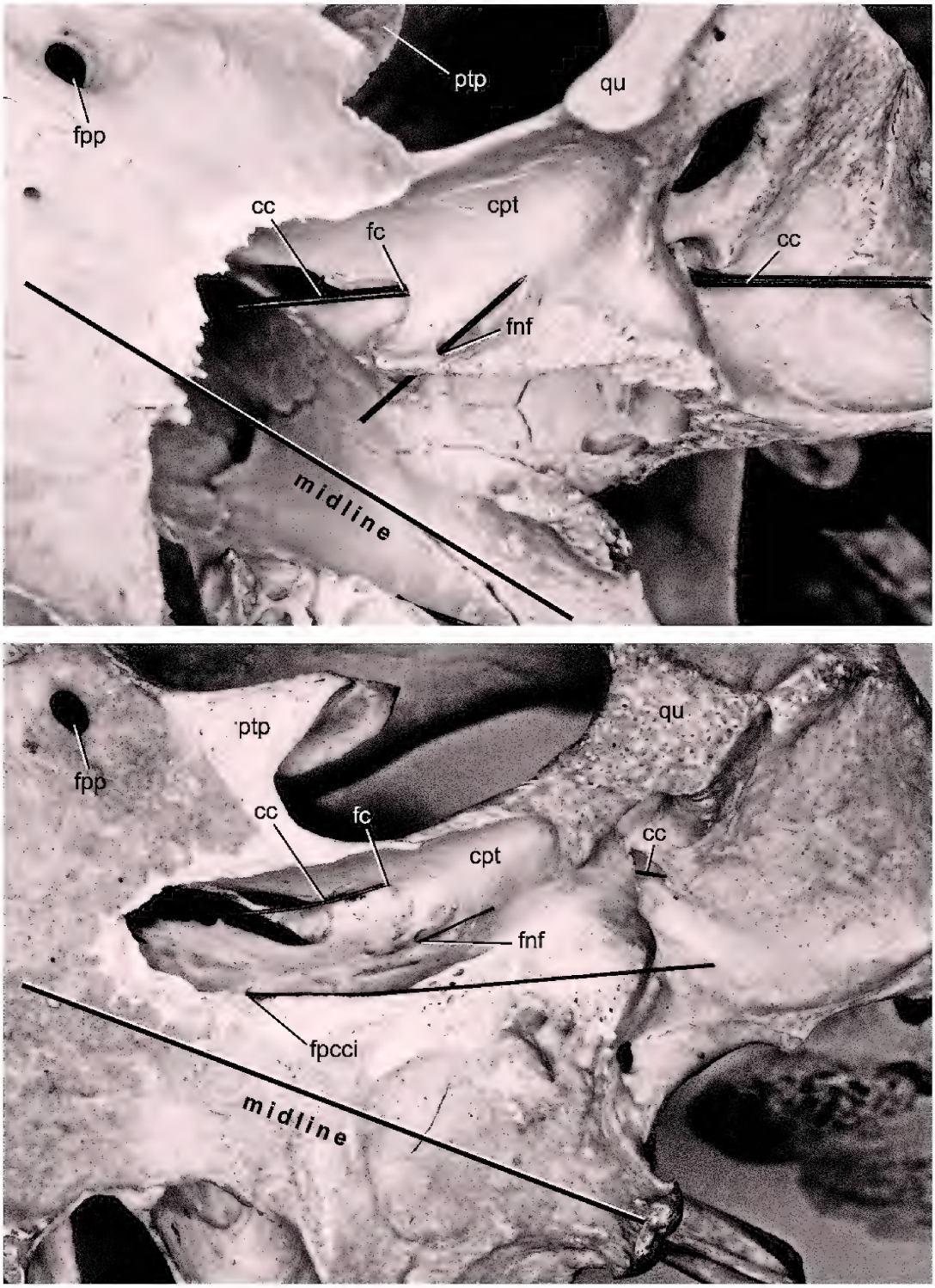



Fig. 41. *Peltocephalus dumerilianus* Schweigger, 1812. Ventral views of left cavum pterygoidi prepared out to show foramina. **Upper,** AMNH Herp R163020; **lower,** NFWFL 338. In both views a probe lies in the canalis cavernosus and the foramen nervi facialis. [E. Gaffney, del.]

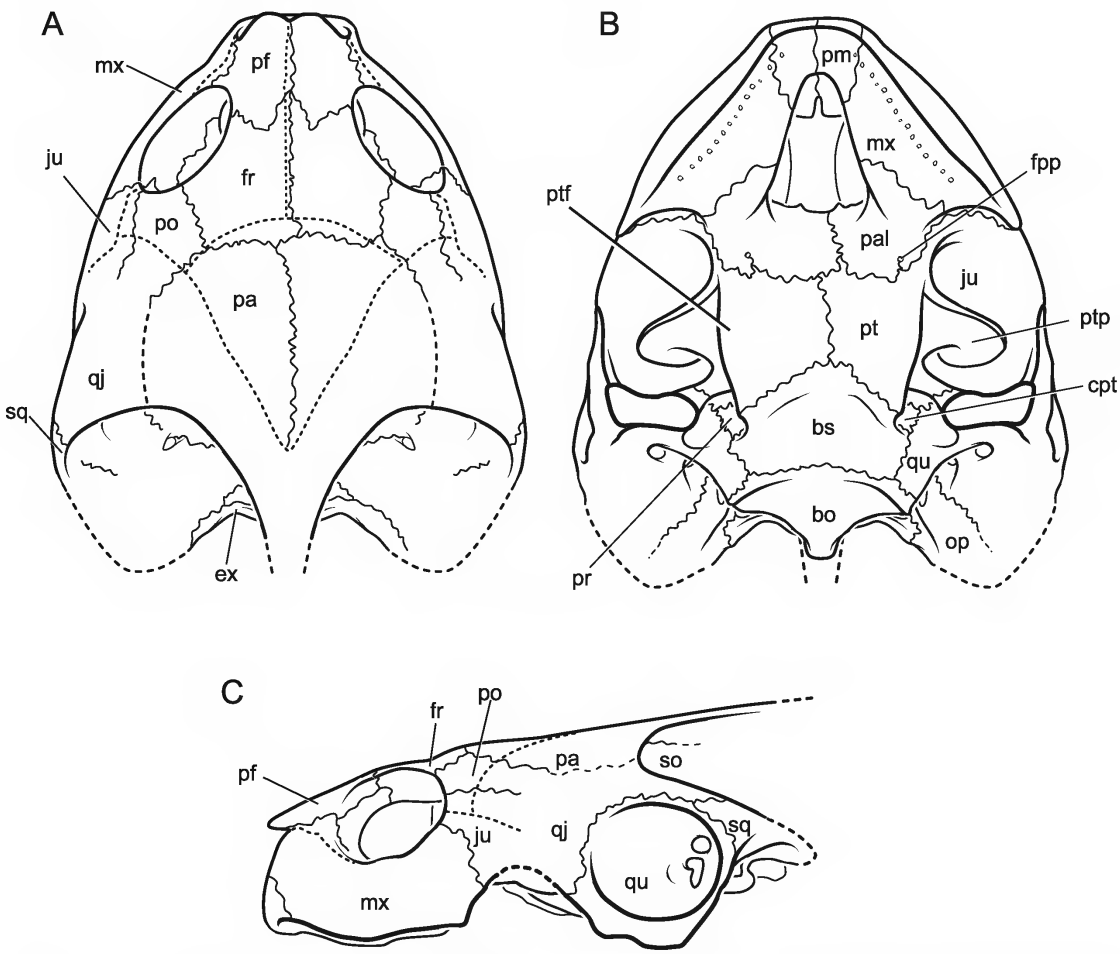



Fig. 42. *Neochelys fajumensis* (Andrews, 1903). Partially restored skull based on DPC 3146. **A,** dorsal; **B,** ventral; **C,** lateral. [C. Facella, del.]

thin. However, a few specimens of *Bauruemys* (e.g., MCZ 4123, figs. 13, 14) show what seems to be a nearly complete flange. Furthermore, specimens of *Pricemys*, *Peiropemys,* and *Lapparentemys* show broken edges and variably preserved flanges that suggest the originals were similar to that in *Podocnemis.*

**Contacts on dorsal surface:** The contacts of the processus trochlearis pterygoidei in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* are with the postorbital dorsolaterally (except in some *Podocnemis*), the jugal anterolaterally and the palatine anteroventrally. The contacts of the crista pterygoidea in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* are with the parietal dorsally.

**Structures on dorsal surface:** As in other pelomedusoides the sulcus palatinopterygoideus in *Lapparentemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* is formed by the parietal dorsomedially, the postorbital (but not in all *Podocnemis*) dorsally, the pterygoid laterally and ventrally, and the palatine ventrally and medially. The foramen nervi trigemini in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* is formed by the parietal dorsally, the prootic posteroventrally, and the pterygoid anteroventrally.

SUPRAOCCIPITAL (figs. 7, 8, 12, 14, 15, 16, 18, 19, 20, 22, 23, 25, 26, 29)

**Contacts:** As in the other pelomedusoides, the contacts in *Lapparentemys, Pricemys*,

Fig. 43. *Neochelys fajumensis* (Andrews, 1903). Partially restored ventral view of skull of DPC 3146. [J. Lovell, del.]

*Peiropemys*, *Bauruemys*, and *Podocnemis* are with the parietals dorsally and anteriorly, the prootic anterolaterally, the opisthotic posterolaterally, and the exoccipitals posteroventrally.

**Structures:** The crista supraoccipitalis is preserved complete in at least one specimen of *Bauruemys* and *Peiropemys,* but the entire length is preserved only in the Broin (1991) "Tiupampa" specimen of *Lapparentemys vilavilensis*. The length of the crista as a function of total skull length varies among the recent species, so it is probably not a useful systematic indicator. *Bauruemys* has a longer crista supraoccipitalis than *Peiropemys* and *Lapparentemys*. Some *Podocnemis expansa* skulls have a crista that is as long or longer. The crista in *Podocnemis* has a ventral thickening that is a variably horizontal bar. Although the material is not really complete enough to be sure about this, *Peiropemys* and *Lapparentemys* have a slightly wider horizontal bar than *Bauruemys*.

There is no apparent difference among *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* in the size or shape of the foramen magnum.

EXOCCIPITAL (figs. 7, 8, 12, 14, 15, 16, 18, 19, 20, 22, 23, 25, 26, 27, 29)

**Contacts:** As in the other Pelomedusoides, the contacts in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* are with the supraoccipital dorsally, the opisthotic laterally, the quadrate ventrolaterally, the basioccipital ventrally, and (in ventral view) the basisphenoid anteriorly.

**Structures:** In *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis,* there are two foramina nervi hypoglossi in each exoccipital. The foramen jugulare posterius is open laterally in *Bauruemys*, and it is closed laterally by the opisthotic in *Lapparentemys*, *Pricemys*, *Peiropemys*, and *Podocnemis*. Although one specimen of *Bauruemys*, MCT 1492-R, apparently has the foramen closed, this seems to be due to dorsoventral crushing, as the well-preserved MCZ 4123 has the foramen open laterally. In the closed example, the closure is due to meeting of the exoccipital, rather than ossification of the opisthotic, more evidence that the condition is postmortem.

BASIOCCIPITAL (figs. 7, 8, 12, 14, 15, 16, 18, 19, 20, 22, 23, 25, 26, 27, 29)

**Contacts:** In *Lapparentemys*, *Pricemys*, *Peiropemys*, and *Podocnemis,* the contacts are with the basisphenoid anteriorly, the quadrate laterally, the exoccipitals posterodorsally, and the opisthotic laterally. The contacts in *Bauruemys* are the same except that in well-preserved specimens it lacks the opisthotic contact. As with the "closed" foramen jugulare posterius, some specimens have a very small basioccipital-opisthotic contact, but this is interpreted as due to slight dorsoventral deformation in this fragile area in these specimens, as it is absent in better preserved specimens like MZC 4123.

**Structures:** In ventral view the basioccipitals in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* are similar in that they have paired tubercula basioccipitale and a median concavity. However, there are differences. In *Bauruemys* the tubercula are relatively short and close together, so that the median concavity is narrow. In *Lapparentemys*, *Pricemys*, *Peiropemys*, and *Podocnemis,* the tubercula are at the lateralmost margin of the basioccipital, at the contact with the opisthotic. The median concavity in these taxa is relatively wide. In *Pricemys*, *Peiropemys,* and most *Podocnemis* (but not in our specimens of *P. sextuberculata and P. erythrocephala*), the tuberculum basioccipitale is extended posterolaterally as a short, horizontal shelf.

PROOTIC (figs. 12, 14, 15, 16, 18, 25, 27, 29)

**Contacts:** The contacts in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* are with the parietal dorsomedially, the quadrate laterally, the supraoccipital posterodorsally, the pterygoid ventrally, and the opisthotic posteriorly.

**Structures:** The prootic in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* is very similar. It forms the dorsal margin of the foramen nervi trigemini with the pterygoid and parietal. It forms the medial portion of the foramen stapediotemporale with the quadrate laterally. The prootic forms a small part of the roof of the cavum pterygoidei and contains the foramen nervi facialis. In contrast to generalized or more "basal" pelomedusoides, the foramen posterius canalis carotici interni is not formed by the prootic in podocnemidids.

OPISTHOTIC (figs. 7, 8, 12, 14, 15, 16, 18, 19, 20, 22, 23, 25, 26, 27, 29)

**Contacts:** The contacts in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* are with the supraoccipital anteromedially, the prootic anteriorly, the quadrate anterolaterally, the squamosal posterolaterally, and the exoccipital posteromedially. In *Lapparentemys*, *Pricemys*, *Peiropemys*, and *Podocnemis,* there is also a ventral contact with the basioccipital.

**Structures:** In *Pricemys*, *Peiropemys*, *Lapparentemys*, and *Podocnemis*, the foramen jugulare posterius is formed laterally by the opisthotic but the foramen is open laterally in *Bauruemys*. The fenestra postotica is open ventrally in *Pricemys*, *Peiropemys*, *Bauruemys*, *Lapparentemys*, and *Podocnemis*, but the low grooves for the lateral head vein (more medial) and the stapedial artery (more lateral, mostly in the quadrate) can be seen in all of them. In some *Podocnemis* there are variably developed processes separating the two structures. The processus interfenestralis is covered

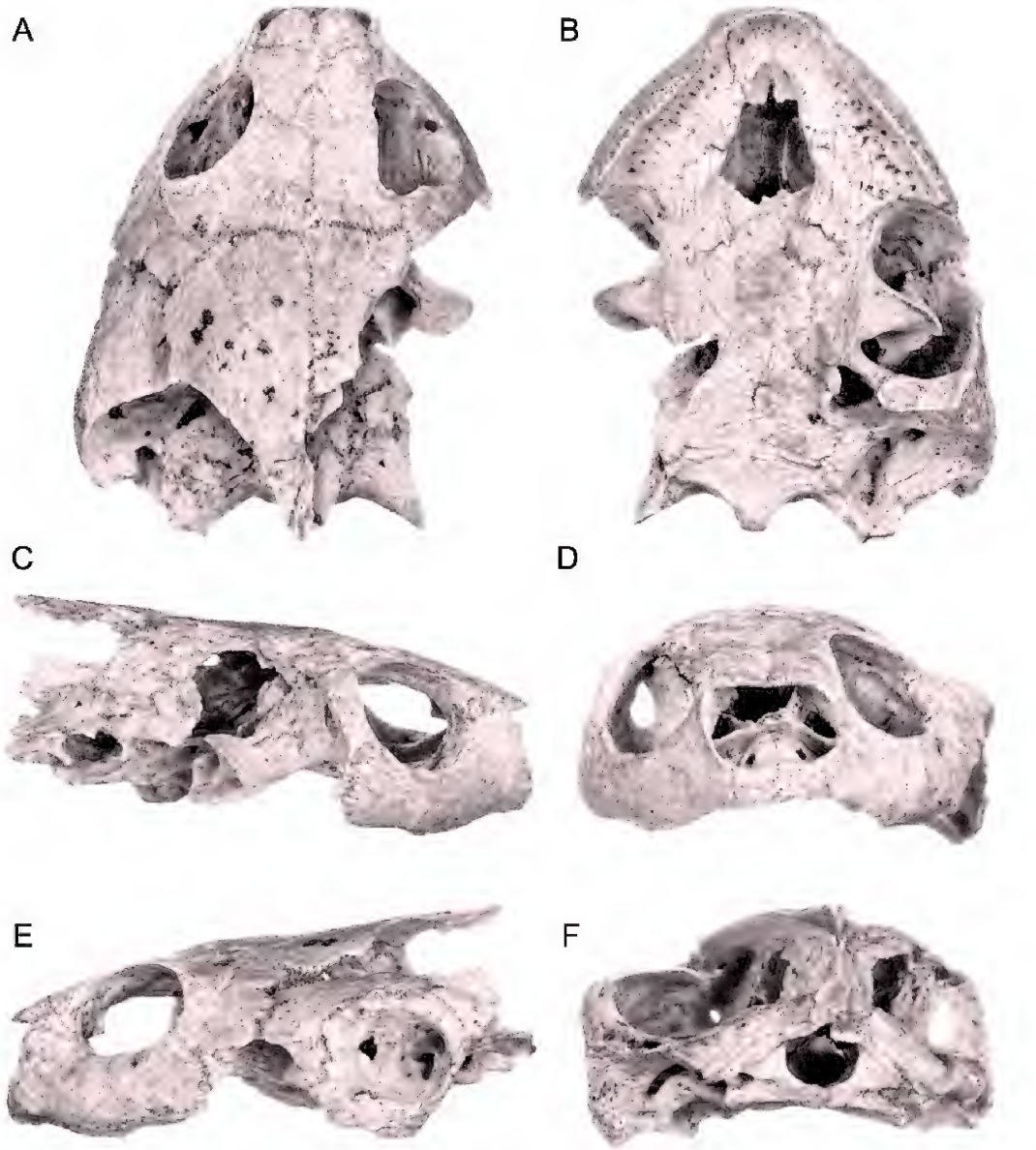



Fig. 44. *Neochelys fajumensis* (Andrews, 1903). DPC 3146. Skull. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [C. Facella, del.]

ventrally in all specimens of *Pricemys*, *Peiropemys*, *Lapparentemys*, and *Bauruemys*, and in all mature specimens of *Podocnemis.*

BASISPHENOID (figs. 7, 8, 12, 14, 15, 16, 18, 19, 20, 22, 23, 25, 26, 27, 29)

**Contacts on ventral surface:** In *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis,* the contacts are with the pterygoids anterolaterally, the basioccipital posteriorly, the prootic laterally, and the quadrate laterally.

**Structures on ventral surface:** The shape of the basisphenoid in *Lapparentemys*, *Pricemys*, *Peiropemys*, *Bauruemys*, and *Podocnemis* is similar but not identical. In *Bauruemys* the outline is more triangular than in *Lapparentemys* and *Peiropemys*, although in

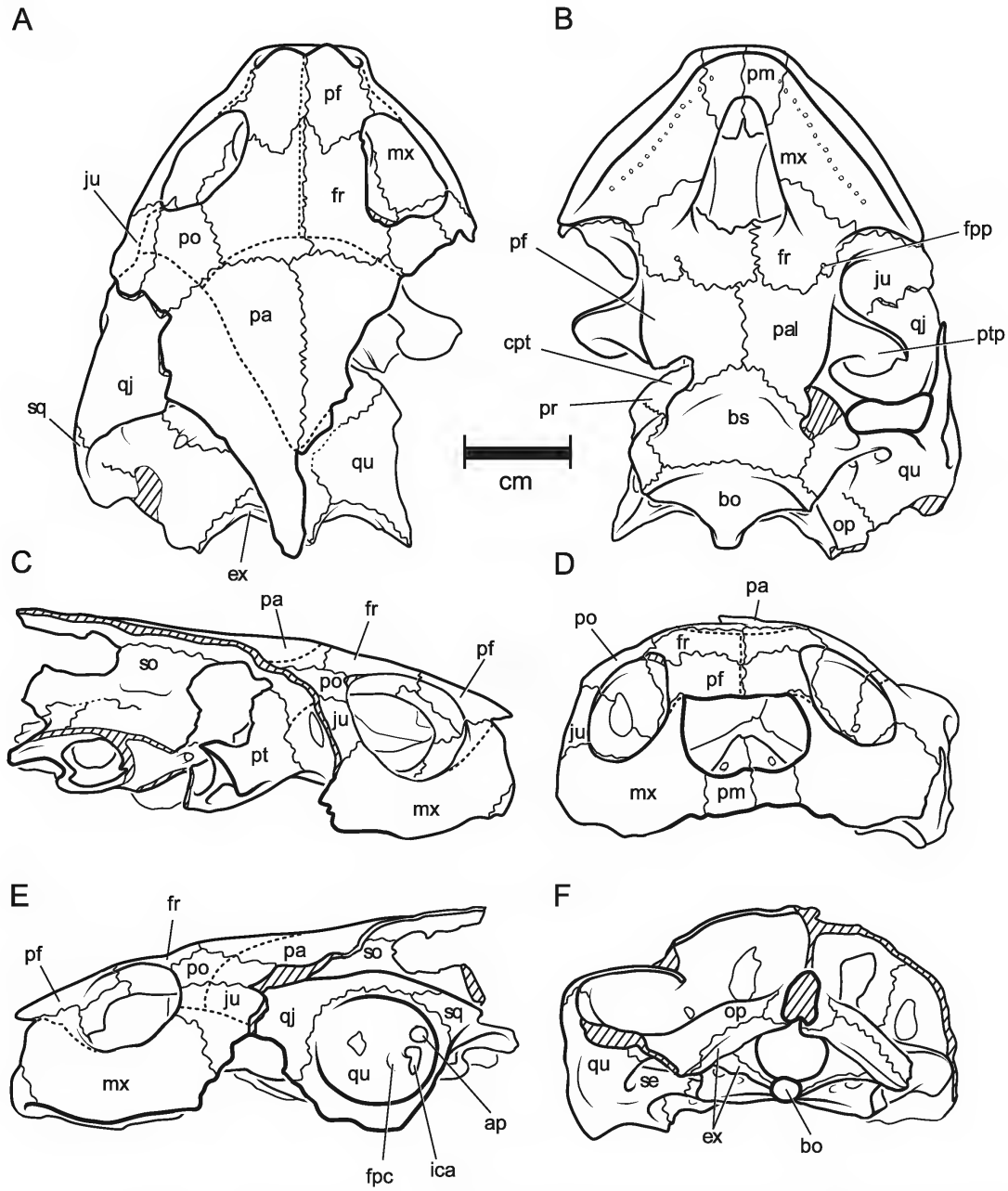



Fig. 45. *Neochelys fajumensis* (Andrews, 1903). DPC 3146. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [C. Facella, del.]

*Podocnemis* there is even greater variation. The cavum pterygoidei (see Pterygoid) is formed medially by the basisphenoid, which also contains the foramen posterius canalis carotici interni.

**Contacts on dorsal surface:** Visible in *Pricemys* and *Bauruemys* the contacts are with the pterygoid anterolaterally, the prootic laterally, the palatines anteriorly, and the basioccipital posteriorly.

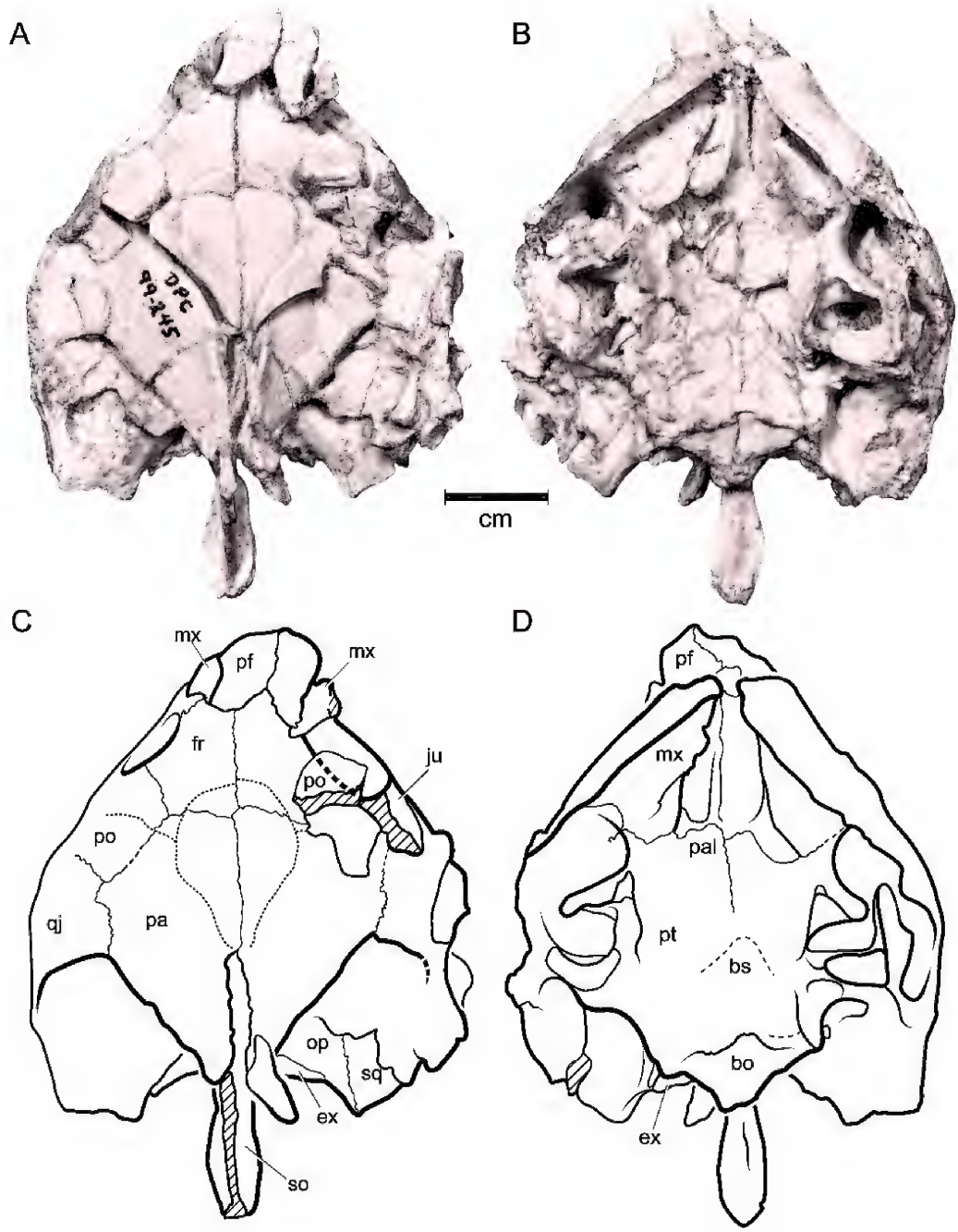



Fig. 46. *Neochelys fajumensis* (Andrews, 1903). DPC 99–245. Skull. **A, C,** dorsal views; **B, D,** ventral views.

**Structures on dorsal surface:** The dorsal surface of the basisphenoid can be seen in *Bauruemys* (AMNH 30643 and AMNH 30642), *Pricemys*, and *Lapparentemys* (Broin, 1991, "Tiupampa"). The shape of the rostrum basisphenoidale, sulcus cavernosus, sella turcica, and dorsum sellae are similar in all three. As in *Podocnemis*, the rostrum is

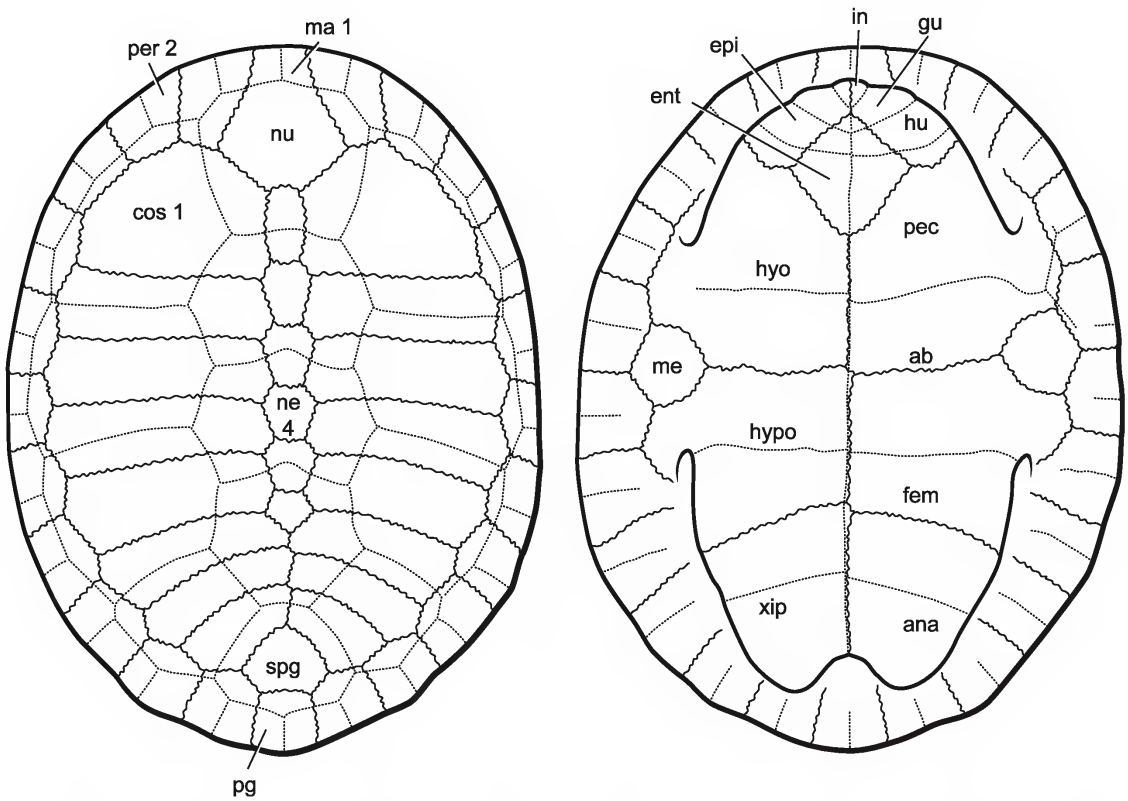



Fig. 47. *Neochelys fajumensis* (Andrews, 1903). Restored shell based on literature, YPM, and AMNH material (see text). Left, dorsal; right ventral. [R. Wood, C. Wilson, del.]

fused, columnar and elongate, and the sella turcica is oval with a distinct overhanging dorsum sellae. In *Lapparentemys*, *Pricemys*, *Peiropemys*, and *Bauruemys*, the canalis caroticum internus is a distinct canal running through a wall of bone from the cavum pterygoidei to the foramen anterius canalis carotici interni, while in *Podocnemis* the canal does not exist, and the foramen anterius canalis carotici interni is the only separation of the cavum pterygoidei and the sella turcica.

DENTARY (fig. 34)

The lower jaws of *Lapparentemys* are well known from the work of Broin (1971: pl. 32, fig. 1b–d; 1991: pl. 2, figs. 6, 7). We also used WUS 2160 and AMNH 14444 for *Lapparentemys;* and for *Bauruemys,* AMNH 30643, and AMNH 30642. A lower jaw possibly assignable to *Pricemys* is DGM MCT without a number (fig. 34).

**Contacts:** The contacts in *Lapparentemys*, *Bauruemys*, and *Podocnemis* are with the coronoid posterodorsally, the surangular posterolaterally, and the angular posteroventrally.

**Structures:** The jaw rami are fused at the symphysis in all podocnemidids, but are sutured in *Euraxemys*. The triturating surface in *Podocnemis* is relatively narrow, compared with many bothremydids, but it is wider posteriorly than in *Euraxemys*. In *Lapparentemys* the triturating surface is narrower anteriorly and wider posteriorly. The labial ridge in *Lapparentemys* begins at the symphysis with a hook, very similar in size and shape to the one seen in *Podocnemis*. The labial ridge in *Lapparentemys* curves ventrally along the jaw ramus to rise dorsally where it meets the processus coronoideus, so that the whole labial ridge forms a shallow, dorsally concave, margin in lateral view. This is very similar to the labial ridge in *Podocne-*

*mis*. The lingual ridge in *Lapparentemys* begins just anterior to the median concavity, which is much larger in *Lapparentemys* than it is in *Podocnemis*. The lingual ridge in *Lapparentemys* curves medially to widen the triturating surface posteriorly so that it is about the same width posteriorly in *Lapparentemys* as it is in *Podocnemis*. As in *Podocnemis* the lingual ridge on *Lapparentemys* rises posteriorly, so that it is higher than the labial ridge in lateral view. A significant difference between *Lapparentemys* and *Podocnemis* is that in *Podocnemis* the lingual ridge is split into accessory ridge or ridges forming a narrow shelf along the medial margin of the triturating surface. In *Lapparentemys*, *Bauruemys*, and ?*Pricemys* the lingual ridge is a single, acute margin with no accessory ridges or shelf. The triturating surface in *Lapparentemys*, *Bauruemys*, and ?*Pricemys* has a shallow concavity along its length, shallower than that seen in *Podocnemis expansa*.

The sulcus cartilaginis meckelii in *Lapparentemys* and *Podocnemis* is a distinct groove posteriorly, as in *Euraxemys*, but anteriorly it widens gradually into the median concavity, not maintaining a separate groove as in *Euraxemys*. The foramen intermandibularis medius is formed laterally by the dentary and medially by the prearticular. In *Podocnemis* it is a narrow notch while in *Lapparentemys* it is broader and relatively more open. The foramen alveolare inferius is formed by the dentary, within the sulcus cartilaginis meckelii, ventral to the coronoid suture, in about the same position in *Lapparentemys*, *Podocnemis*, and *Euraxemys*. On the lateral surface the foramen dentofaciale majus lies at the posterior edge of the triturating surface, just below the processus coronoideus in *Lapparentemys* and *Podocnemis*. In *Euraxemys* the foramen is more ventral and separated from the labial ridge.

ANGULAR

**Contacts:** The contacts in *Lapparentemys* and *Podocnemis* are with the dentary anteriorly, the prearticular dorsomedially, the articular posteriorly, and the surangular dorsolaterally. However, in nearly all *Podocnemis* the angular, surangular, articular, and prearticular are fused wholly or partially, so that sutures are rarely visible except in juveniles. The close similarity of *Lapparentemys* to *Podocnemis* allows description of comparable areas even without sutures as a landmark.

**Structures:** The angular in *Lapparentemys* and *Podocnemis* forms the ventral margin of the posterior part of the sulcus cartilaginis meckelii. The foramen intermandibularis caudalis, as seen in *Euraxemys* and other pleurodires, is absent in *Lapparentemys* and *Podocnemis*.

SURANGULAR

**Contacts:** The contacts in *Lapparentemys* and presumably in *Podocnemis*, are with the dentary anteriorly, the coronoid anterodorsally, the angular posteroventrally, and the articular posteromedially.

**Structures:** The fossa meckelii in *Lapparentemys* and *Podocnemis* is formed laterally by the surangular and medially by the prearticular. It is relatively narrow and about as extensive as in *Euraxemys* in contrast to the wider and larger fossa usually seen in bothremydids. The dorsal opening of the fossa is also narrow in *Lapparentemys* and *Podocnemis*. In *Lapparentemys* it is more posterior and closer to the area articularis mandibularis than in *Podocnemis*. The opening of the fossa meckelii is oriented posterodorsally in *Lapparentemys* rather than more dorsally, as in *Podocnemis*.

The foramen nervi auriculotemporalis of *Podocnemis* is a complex space (possibly unique to the Podocnemididae; see also Gaffney et al., 1998) that communicates between the external surface of the surangular and the internal surface, within the fossa meckelii. Although the lateral openings of this foramen are preserved in *Lapparentemys*, the internal one is probably covered by matrix on one side and bone on the other. A surangular-articular suture can be seen on the anterior edge of the area articularis mandibularis and seems to indicate that the surangular makes up the lateral third of the surface, similar to what is seen in juvenile *Podocnemis*, as it is fused in adults.

In *Lapparentemys* the processus coronoideus is very low, barely rising above the rest of the jaw, in contrast to outgroups such as *Euraxemys* and bothremydids. Just posterior

to the coronoid bone is a process formed by the surangular that is nearly as high as the processus coronoideus. In *Podocnemis* this surangular process is actually higher than the low cone on the coronoid, and appears at first glance to be the actual processus coronoideus. The actual attachment site of the main adductor tendon is not known by us at present. The processus retroarticularis in podocnemidids is depressed and separated below the level of the area articularis mandibularis, and this is seen in *Lapparentemys*, ?*Pricemys*, and *Bauruemys*, similar to *Podocnemis* itself. The surangular forms the lateral surface of this process.

CORONOID

**Contacts:** The contacts in *Lapparentemys* and *Podocnemis* are with the dentary anteriorly and laterally, the surangular posterolaterally, and the prearticular posteromedially.

**Structures:** As discussed above, the processus coronoideus of recent *Podocnemis* is lower and smaller than the process, posterior and lateral to it, seen on the surangular. In *Lapparentemys* both processes are comparable in size and the surangular one is lower than the coronoid one. The coronoid bone extends slightly onto the triturating surface, as in *Euraxemys* and pelomedusids, but not to the extent seen in many bothremydids. The anterior part of the fossa meckelii is formed by a narrow exposure of the coronoid.

ARTICULAR

**Contacts:** Even in well-preserved specimens of *Lapparentemys*, many of the articular sutures are fused. However, based on what is preserved, it is likely that the contacts are with the surangular laterally, the angular anteroventrally, and the prearticular medially, as in other pelomedusoids.

**Structures:** The surface of the area articularis mandibularis in *Lapparentemys* is very similar to that in *Podocnemis*. The posterior end of the jaw below the area articularis mandibularis is slightly thinner in lateral view than in *Podocnemis*. The processus retroarticularis in *Lapparentemys* is slightly shorter than in *Podocnemis* but has the same posteroventral orientation. The size of the tendon attachment area, to the extent that this can be identified, appears to be less in *Lapparentemys* than in *Podocnemis*. The articular has a slight exposure in the posterior part of the fossa meckelii in both *Lapparentemys* and *Podocnemis*. The foramen posterius chorda tympani lies on the medial surface of the articular (possibly the angular in *Podocnemis*), just below the edge of the area articularis mandibularis in both *Lapparentemys* and *Podocnemis,* rather than on the surface of the area as in *Euraxemys*.

PREARTICULAR

**Contacts:** The contacts in *Lapparentemys* are with the coronoid anterodorsally, the articular posteromedially, and the angular ventrally. In *Podocnemis* many of these sutures are fused but these same contacts are likely.

**Structures:** The fossa meckelii is covered medially by the thin sheet of prearticular. At the anterior end of the bone, the prearticular forms the margin of the foramen intermandibularis medius, the anterior opening of the fossa meckelii. In *Lapparentemys* and *Podocnemis* this opening lies in about the same position as it does in *Euraxemys*. The foramen intermandibularis caudalis is apparently absent in *Podocnemis* and in *Lapparentemys*, although we are not completely certain of the identification of small foramina in the dried skull.

## CRANIAL MORPHOLOGY OF THE TRIBE STEREOGENYINI

The skulls of the species of *Bairdemys* have already been described and figured in detail (Gaffney and Wood, 2002; Gaffney et al., 2008), and these will not be repeated here. It is assumed that the reader is familiar with and has available these papers, which are relied upon for comparisons in the descriptions below.

### *Mogharemys*

Figures 48–51

PREFRONTAL

**Preservation:** The prefrontal is missing in BMNH R.8440. However, it is present in the figure (Dacqué, 1912: fig. 12, actually a figure of the cast, see discussion under *Mogharemys* in Systematics) and the more complete cast (MB. R. 2860) of BMNH R.8440 used by Dacqué.

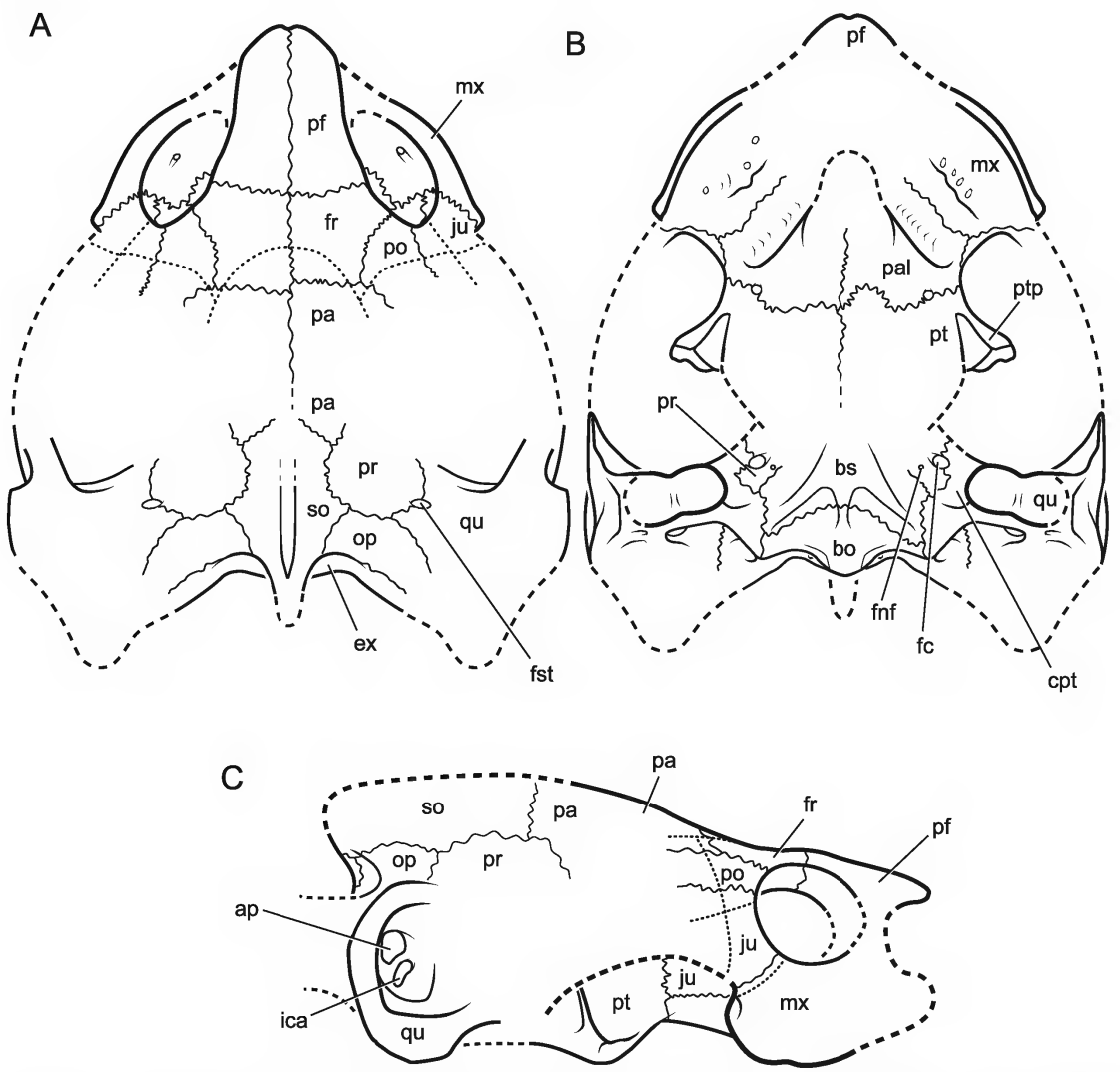



Fig. 48. *Mogharemys blanckenhorni* Dacqué (1912), n. gen. Partially restored skull based on BMNH R8440 and MB.R.2860 (cast of BMNH R8440). **A,** dorsal; **B,** ventral; **C,** lateral. [F. Ippolito, del.]

**Contacts:** In the cast the prefrontal has the usual contact with the frontal posteriorly in a position similar to that in *Shweboemys pilgrimi* so that the prefrontal forms the anterodorsal part of the orbital margin. The cast seems to have a ventral process contacting the maxilla, as in other podocnemidids. The presence or absence of a palatine contact is not determinable in the cast.

**Structures:** In MB. R. 2860 the prefrontal is longer on the midline than the frontal, being more similar in that feature to *Shweboemys* than to the other subtribe Stereogenyina, which have relatively shorter prefrontals. The prefrontal in MB. R. 2860 has a curved, slightly protuberant, anterior margin, as in *Bairdemys* and *Podocnemis*.

FRONTAL

**Preservation:** Both frontals are present in BMNH R.8440, but lack their anterior margins. The anterior contacts with the prefrontals are preserved in the cast, MB. R. 2860.

**Contacts:** The frontal contacts the other frontal on the midline, the postorbital posterolaterally, the parietal posteriorly, and the palatine ventrolaterally in the septum

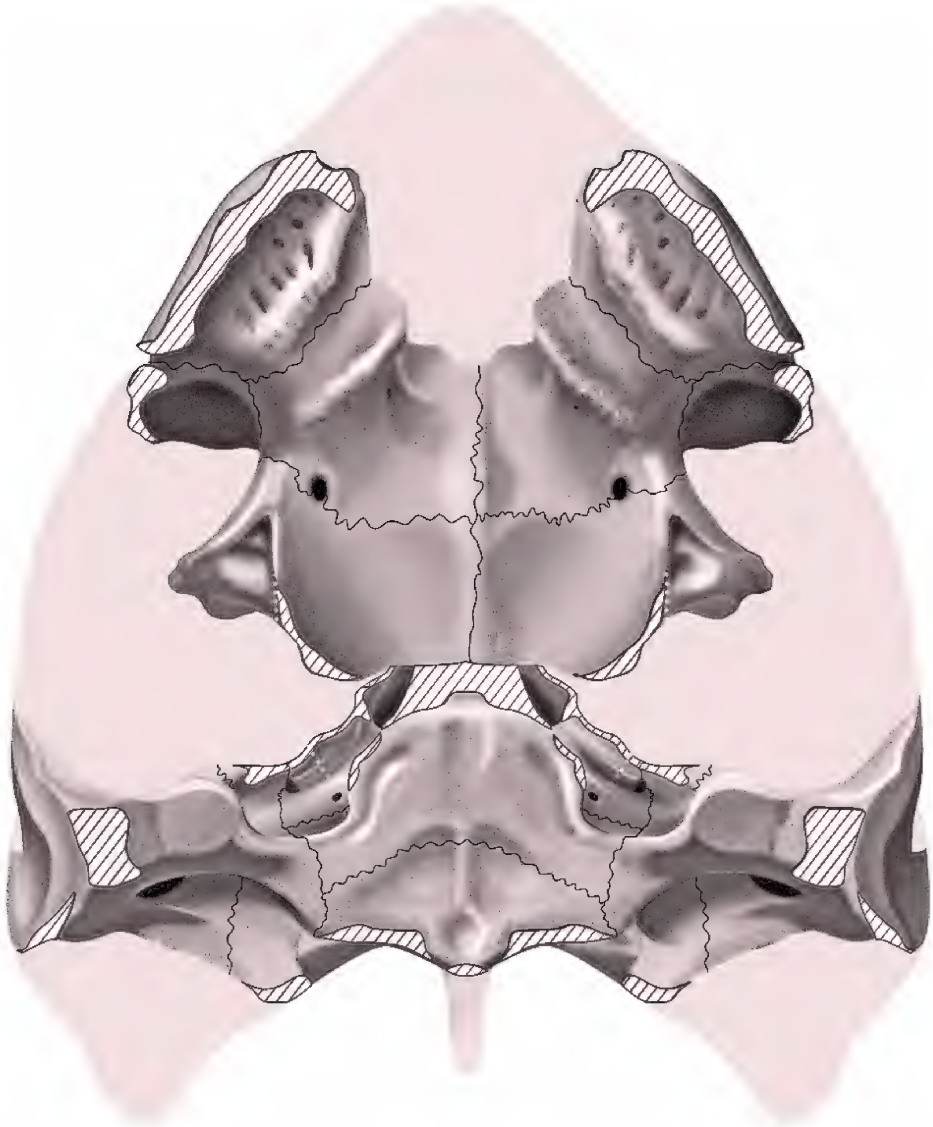


Fig. 49. *Mogharemys blanckenhorni* Dacqué (1912), n. gen. Partially restored ventral view based on BMNH R8440. [F. Ippolito, del.]

orbitotemporale (broken away on the left side of BMNH R.8440).

**Structures:** The frontal of *Mogharemys* as seen in MB. R. 2860 is wider than long, differing from most subtribe Stereogenyina, which are equidimensional or longer than wide. The frontal forms the dorsal part of the orbital margin and is exposed in the anterior wall of the septum orbitotemporale much as seen in *Erymnochelys*. The frontal roofs the anterior part of the sulcus orbitotemporale, as in most pelomedusids.

PARIETAL

**Preservation:** Portions of both parietals are preserved in both the anterior and posterior moieties of BMNH R.8440. In the Berlin cast the anterior part of both parietals are preserved, overlapping with the anterior moiety of BMNH R.8440. All of the temporal roofing is absent in both specimens and only the anterior limits of the parietal on the skull roof can be seen. The anterior portion of the processus inferior parietalis is preserved in the anterior moiety and the posteriormost part of

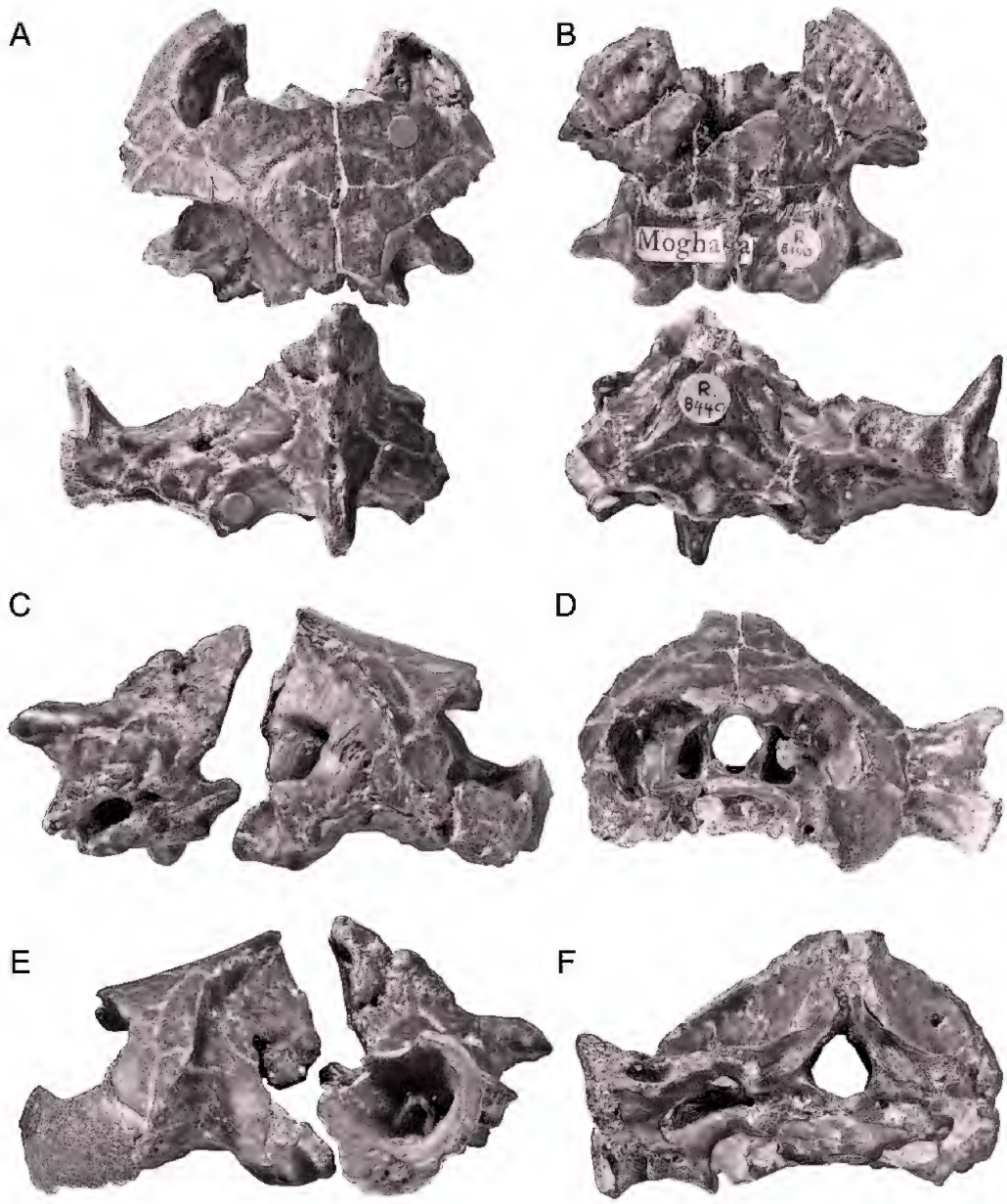



Fig. 50. *Mogharemys blanckenhorni* Dacqué (1912), n. gen. BMNH R8440. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [C. Facella, del.]

the parietal is present on the posterior moiety, although damaged on the surface. None of the skull roof is preserved on the posterior moiety of BMNH R.8440.

**Contacts of dorsal plate:** The parietal in BMNH R.8440 contacts the other parietal on the midline. The frontal anteriorly and the postorbital laterally. The other skull roof contacts are not preserved.

**Structures of dorsal plate:** Neither BMNH R.8440 nor the Berlin cast show any indications of the skull roof margins. The sulcus palatinopterygoideus is roofed posteriorly by the parietal as in most pelomedusoides.

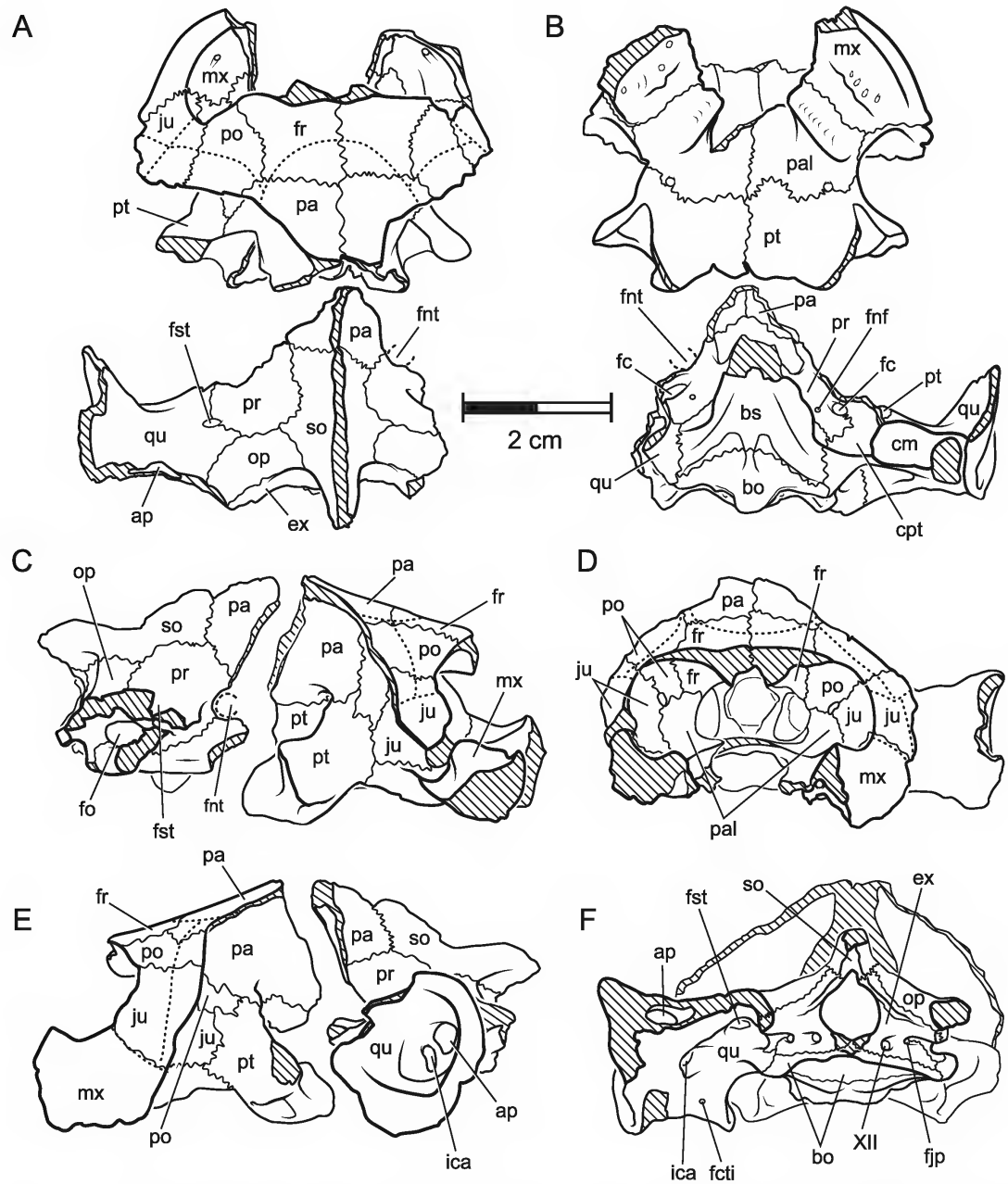



Fig. 51. *Mogharemys blanckenhorni* Dacqué (1912), n. gen. BMNH R8440. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [C. Facella, del.]

**Contacts of processus inferior parietalis:** Although incomplete, the processus in *Mogharemys* contacts the palatine anteroventrally, the pterygoid ventrally, the prootic posteroventrally and the supraoccipital posteriorly, as in other pelomedusoides.

**Structures of processus inferior parietalis:** Only a small part of the margin of the foramen nervi trigemini is preserved on the right side of BMNH R.8440. It shows the parietal forming the more dorsal margin and the pterygoid the more ventral margin, as in

most pelomedusoides. Although the prootic on both sides of the posterior moiety preserves some of the foramen nervi trigemini, it does not preserve the parietal contact.

JUGAL

**Preservation:** The anterior part of the jugal is preserved on both sides of BMNH R.8440, but the posterior limits of the lateral plate are missing.

**Contacts of lateral plate:** The preserved contacts in *Mogharemys* are with the maxilla anteroventrally and the postorbital dorsally. The posterior margin on both sides is a broken edge.

**Structures of lateral plate:** The jugal in *Mogharemys* widely enters the orbit and forms most of its posterior margin. The preserved posterior edge of the jugal and maxilla are broken, but the bone is thin and as some of the margin is smooth, probably due to abrasion rather than a natural edge, a cheek emargination close to the preserved edge is possible.

**Contacts of medial process:** In the floor of the orbit in dorsal view, the jugal contacts the maxilla anteriorly and laterally and the palatine medially, as in most other pelomedusoides. In the septum orbitotemporale, in posterior view, the jugal contacts the postorbital dorsomedially, the palatine ventromedially, the pterygoid posteroventrally, and the maxilla ventrally, as in most pelomedusoides.

**Structures of medial process:** The jugal in *Mogharemys* forms only a small part of the fossa orbitalis floor, but a significant part of the septum orbitotemporale. It does not enter the triturating surface.

QUADRATOJUGAL

The quadratojugal is not preserved in either BMNH R.8440 or the Berlin cast.

SQUAMOSAL

The squamosal is not preserved in either BMNH R.8440 or the Berlin cast.

POSTORBITAL

**Preservation:** The postorbitals on both sides of BMNH R.8440 lack the posterior plate, so its extent in the skull roof in unknown. The Berlin cast is broken to a similar extent.

**Contacts of lateral plate:** The contacts in *Mogharemys* are with the frontal anteromedially, the jugal ventrally, the parietal posteromedially, and the maxilla anteroventrally, as in most pelomedusoides.

**Structures of lateral plate:** The postorbital in *Mogharemys* forms the posterodorsal edge of the orbital margin.

**Contacts of medial process:** In the septum orbitotemporale, in anterior view, the postorbital contacts the frontal dorsomedially, the jugal ventrolaterally, and the palatine ventrally. In the septum orbitotemporale, in posterior view, the postorbital contacts the parietal dorsomedially, the pterygoid ventromedially, and the jugal ventrolaterally.

**Structures of medial process:** The medial process of the postorbital in *Mogharemys* forms part of the roof and lateral wall of the sulcus palatinopterygoideus and the septum orbitotemporale, as in most pelomedusoides.

PREMAXILLA

The premaxilla is not preserved in either BMNH R.8440 or the Berlin cast.

MAXILLA

**Preservation:** The maxilla in BMNH R.8440 is present on both sides, but both lack their anterior limits and have no indication of a premaxilla contact. The left maxilla is more complete than the right. Both lack some of the labial ridge. The restored ventral view shows the complete extent to which the maxilla is known to combine both sides. Interestingly, the Berlin specimen provides no more information and has breakage very similar to that seen in BMNH R.8440.

**Contacts of vertical plate:** The only contact known for the vertical part of the maxilla in *Mogharemys* is with the jugal posterodorsally. In the Berlin cast, it is likely that the complete orbit on the right side has the dorsal process of the maxilla that contacts the prefrontal.

**Structures of vertical plate:** The outer edge of the maxilla in *Mogharemys* curves anteromedially to a greater extent than in *Podocnemis*, *Erymnochelys*, and *Peltocephalus*, but similar to the curve in *Stereogenys* and *Shweboemys*, indicating a relatively wide snout. The maxilla forms the ventral margin for the orbit. There is a distinct lip along

the margin as in *Cordichelys*, not a smooth, rounded edge as in *Brontochelys*.

**Contacts of horizontal plate:** The maxilla of *Mogharemys* contacts the palatine posteromedially and the jugal posterolaterally.

**Structures of horizontal plate:** As preserved, the maxilla of *Mogharemys* does not form part of the apertura narium interna margin, but it is broken away anteriorly where this would be expected. The labial ridge of BMNH R.8440 is broken along all of its length, but it is sufficiently well preserved to show that it had a relatively narrow and acute margin. This margin is not very deep, in comparison to the condition in subtribe Stereogenyina like *Stereogenys*. The Berlin cast, MB. R. 2860, is preserved to almost the same extent as BMNH R.8440, and does not show any more of the maxilla. The triturating surface is wide but, as noted by Williams (1954c), there is no secondary palate in *Mogharemys*. The maxilla bears a secondary or accessory ridge parallel to the labial ridge. This accessory ridge is deeper and wider than those seen in *Podocnemis*, and has a very rugose surface seen in both specimens. The maxilla makes up over half of the triturating area surface. The palatine makes up about a third of the surface as preserved. There is no contribution from the jugal.

Although many podocnemidids have accessory ridges of varying sizes, the maxillary ridge seen in BMNH R.8440 and its cast, MB. R. 2860, is relatively broader than those seen in *Podocnemis*, for example. The more medial accessory ridge is formed entirely by the palatine and, parallel to the accessory ridge of the maxilla, is deeper and blunter then the accessory ridge. This combination in *Mogharemys* of a more massive medial maxillary ridge with a smaller but still prominent accessory ridge is unique among the Podocnemididae. *Dacquemys* (Dacqué, 1912; Gaffney et al., 2002) also has two prominent ridges but the more lateral accessory ridge is larger than the medial ridge.

On the dorsal surface the maxilla forms the lateral part of the floor of the fossa orbitalis as in other podocnemidids.

VOMER

There is no evidence for the presence or absence of a vomer as the area is not preserved in either the actual specimen or its cast.

PALATINE

**Preservation:** Both palatines are preserved in BMNH R.8440 and are complete except for their anteromedial margins.

**Contacts:** In ventral view the palatine in *Mogharemys* contacts the maxilla anterolaterally, the other palatine medially on the midline, and the pterygoid posteriorly. In the floor of the fossa orbitalis the palatine also contacts the maxilla anterolaterally and the jugal laterally. A dorsal process of the palatine in the septum orbitotemporale (the posterior wall of the fossa orbitalis), contacts the postorbital dorsally and the frontal dorsomedially. The palatine contacts the ventral margin of the processus inferior parietalis of the parietal.

**Structures on dorsal surface:** The palatine of *Mogharemys* forms the medial part of the fossa orbitalis and the floor of the anterior part of the sulcus palatinopterygoideus, as in most other pelomedusids. The foramen palatinum posterius is mostly formed by the palatine and lies in the palatine-pterygoid suture, as in most pleurodires. The posterior extension of the fossa orbitalis past the level of the orbital rim seen in subtribe Stereogenyina is absent in BMNH R.8440.

**Structures on ventral surface:** The palatine of *Mogharemys* forms the lateral wall and roof of the choanal passage, but only its more posterior part is preserved. The choanal passage in BMNH R.8440 has a thickened margin along its ventrolateral margin, unlike the thin edge seen in *Podocnemis*. There is no indication, however, of a secondary palate or even a partial secondary palate. The palatine, however, is thicker and wider in BMNH R.8440 than in taxa outside the subtribe Stereogenyina, and this might bea character in common although we have not used it here due to its variability in turtles in general.

The palatine forms about a third of the triturating surface as preserved in BMNH R.8440. It forms a heavy, deep ridge parallel to the maxillary contact and the accessory ridge on the maxilla. The ridge is deeper than in *Dacquemys* and *Podocnemis*.

QUADRATE

**Preservation:** The posterior moiety of BMNH R.8440 preserves most of the left quadrate, lacking only the anterior part of the cavum tympani. A fragment of the right quadrate is present, adjacent to the basisphenoid and basioccipital contact. The condylus mandibularis in BMNH R.8440 is eroded posterolaterally, but the more medial part of the surface is preserved.

**Contacts on lateral surface:** No part of the cheek bones or squamosal remain, so none of the lateral surface quadrate contacts can be determined.

**Structures on lateral surface:** The cavum tympani in *Mogharemys* is a deep, cone-shaped cavity, as seen in *Erymnochelys* and *Peltocephalus* and in contrast to the shallower one in *Podocnemis*. The incisura columellae auris is enclosed in an oval opening along with the eustachian tube, as in other podocnemidids. The eustachian tube pathway is not separated from the fenestra postotica as in *Bairdemys*. The antrum postoticum is moderate in size, comparable to that in *Podocnemis*, smaller than in pelomedusids but larger than in such subtribe Stereogenyina forms as *Bairdemys*. Although the anterior part of the cavum tympani is missing, enough is preserved to show that the fossa precolumellaris is absent and the area of the cavum here is smooth.

**Contacts on dorsal and anterior surface:** As in other pleurodires, the quadrate in *Mogharemys* contacts the prootic anteromedially, the opisthotic posteromedially, the supraoccipital medially, and, presumably although it is absent, the squamosal posteriorly and posterolaterally.

**Structures on dorsal and anterior surface:** The foramen stapedio-temporale lies on the dorsal surface of the otic chamber formed between the quadrate and prootic as in other podocnemidids.

**Contacts on ventral surface:** The preserved contacts of the quadrate in *Mogharemys* are with the basisphenoid medially, the basioccipital posteromedially, and the prootic dorsomedially (not usually visible in the ventral view in a podocnemidid, but the pterygoid is broken away in this specimen).

**Structures on ventral surface:** The condylus mandibularis in *Mogharemys* lies just anterior to the level of the condylus occipitalis, as in most subtribe Stereogenyina and in contrast to *Bairdemys*, *Podocnemis*, *Erymnochelys*, and *Peltocephalus*, which have the condylus mandibularis relatively farther anterior.

The cavum pterygoidei in *Mogharemys* is formed laterally and dorsally by the quadrate as in other podocnemidids, and this is can be seen in BMNH R.8440. The lateral extent of the cavum, however, is much deeper in BMNH R.8440 than in other podocnemidids, such as *Podocnemis* and *Peltocephalus*, but it is similar to that in *Erymnochelys* and *Neochelys*. Unfortunately, the cavum pterygoidei depth varies too much to use it as a character within the Podocnemididae. In the roof of the cavum pterygoidei is the foramen cavernosum, formed mostly by the prootic but with some quadrate entering into its margin. Just ventromedial to the foramen cavernosum is a much smaller foramen, the foramen nervi facialis, further discussed under *Lapparentemys* and *Pricemys* and in the character list.

**Contacts on posterior surface:** As preserved the quadrate in BMNH R.8440 contacts the opisthotic dorsomedially, the basioccipital ventromedially, the prootic anteromedially, and a very small contact with the exoccipital medially.

**Structures on posterior surface:** Part of the posterior edge of BMNH R.8440 is eroded, but the fenestra postotica is preserved intact. It is similar to that opening in *Erymnochelys*, *Neochelys*, and *Peltocephalus* in size and shape. There is no separation of the eustachian tube by bone as in some subtribe Stereogenyina. The aditus canalis stapedio-temporalis is large and opens into the nearby canalis stapedio-temporalis. The columella auris of *Mogharemys* lies in a distinct groove running from the incisura columellae auris to the fenestra ovalis, as in most other podocnemidids. The foramen chorda tympani inferius is probably a small foramen just below the eustachian tube groove.

PTERYGOID

**Preservation:** The pterygoid is preserved mostly in the anterior moiety of BMNH R.8440. The posterior moiety has a small portion of the suture with the pterygoid along the left edge of the basisphenoid, and

there is a fragment of left pterygoid on the medial edge of the condylus occipitalis. The anterior moiety has most of both pterygoids, lacking most of the pterygoid flange and the posterior edge. Some of the left processus trochlearis pterygoidei is damaged.

**Contacts on ventral surface:** As in other pleurodires the pterygoid of *Mogharemys* contacts the palatine anteriorly, and the other pterygoid anteromedially. The basisphenoid and quadrate contacts are presumed to have been in the damaged areas.

**Structures on ventral surface:** The processus trochlearis pterygoidei in *Mogharemys* lies at right angles to the midline as in most podocnemidids, and has a small, ventrally opening pocket at its base, as seen in *Peiropemys* and some subtribe Stereogenyina. As in all podocnemidids, BMNH R.8440 has a cavum pterygoidei, but the pterygoid contribution to this is missing and the cavum is open ventrally. The pterygoid flange, usually associated with the cavum, is broken away, but its presence is visible in its base, which is still preserved on both anterior and posterior moieties. The foramen palatinum posterius lies in the palatine-pterygoid suture but is only barely formed by the pterygoid.

**Contacts on dorsal surface:** In the posterior wall of the septum orbitotemporale in *Mogharemys*, the pterygoid contacts the postorbital dorsolaterally, the jugal anterolaterally, the palatine anteroventrally, and the parietal anterolaterally, as in the subtribe Stereogenyina, but not as in *Podocnemis*. The crista pterygoidea is only partially preserved and what is preserved only contacts the parietal.

**Structures on dorsal surface:** The sulcus palatinopterygoideus is formed in *Mogharemys* by the pterygoid and palatine ventrally, along with the parietal and postorbital more dorsally. The crista pterygoidea is relatively high in BMNH R.8440, as in the subtribe Stereogenyina, not low as in *Podocnemis*. It is missing in the area of the foramen nervi trigemini but probably entered its margin based on the remaining bones preserved. The sulcus cavernosus in BMNH R.8440 is wider than in *Podocnemis*, similar to that in some subtribe Stereogenyina.

SUPRAOCCIPITAL

**Preservation:** The supraoccipital is preserved only in the posterior moiety of BMNH R.8440. The crista supraoccipitalis is almost completely missing but a short part of its base remains over the foramen magnum.

**Contacts:** As in other pleurodires the contacts of the supraoccipital in *Mogharemys* are with the parietal dorsally and anteriorly, the prootic anterolaterally, the opisthotic posterolaterally, and the exoccipital posteroventrally.

**Structures:** The supraoccipital in *Mogharemys* is much like that bone in other podocnemidids, and is very similar to that bone in *Podocnemis*.

EXOCCIPITAL

**Preservation:** Both exoccipitals are present in the posterior moiety and are complete except for some abrasion on posterior edges.

**Contacts:** As in other pleurodires, the exoccipital in *Mogharemys* contacts the supraoccipital dorsally, the opisthotic laterally, and the basioccipital ventrally. It also has a narrow contact with the quadrate ventrolaterally, absent in *Podocnemis* but present in *Cordichelys* and *Latentemys*. We have not used this feature as a character as the contact does vary individually and the presence or absence of the contact is extremely close in some specimens. We feel that larger sample sizes for the recent taxa would be needed to support its use.

**Structures:** The exoccipital in *Mogharemys* agrees with the subtribe Stereogenyina in having the two internal foramina nervi hypoglossi join as they leave the skull to form a single, recessed foramen. The condylus occipitalis is damaged, but it can be seen in its base that it is formed by both exoccipitals and the median basioccipital. As in the other podocnemidids the exoccipital closes laterally to form a complete foramen jugulare posterius. The exoccipital forms the medial margin of the fenestra postotica.

BASIOCCIPITAL

**Preservation:** Although there is some breakage along the posteroventral margin and the condylus occipitalis is incomplete, the basioccipital in BMNH R.8440 is otherwise complete.

**Contacts:** The basioccipital of *Mogharemys* contacts the basisphenoid anteriorly, the quadrate laterally, and the exoccipital posterodorsally. Although not entirely clear, there does not seem to be an opisthotic contact.

**Structures:** The basioccipital forms the median bone in the tripartite condylus occipitalis. The tuberculum basioccipitale is small as in the subtribe Stereogenyina and not protruding as in *Podocnemis*. There is no concavity on the ventral surface, which is basically flat. The relative length of the basioccipital is intermediate and similar to that in *Cordichelys* and *Latentemys*, not very long as in *Podocnemis* and not very short as in *Stereogenys*.

PROOTIC

**Preservation:** Both prootics are present and nearly complete in BMNH R.8440.

**Contacts:** As in other podocnemidids the prootic in *Mogharemys* contacts the parietal dorsomedially, the basisphenoid ventrally, the supraoccipital posterodorsally, and the opisthotic posteriorly. There is a presumed contact with the pterygoid anteroventrally, but this is not preserved.

**Structures:** The prootic of *Mogharemys* forms the posterodorsal margin of the foramen trigemini, as in most turtles. The other elements forming the foramen are missing in BMNH R.8440 but the remaining morphology suggests that they are the usual suspects, the parietal and pterygoid. Dorsally the prootic forms the medial margin of the foramen stapedio-temporale and the more interior, canalis stapedio-temporalis. The position of these structures in BMNH R.8440 is similar to those in *Podocnemis* and other podocnemidids.

The prootic of BMNH R.8440 is widely exposed in the cavum pterygoidei and its morphology indicates that *Mogharemys* has a widely open cavum pterygoidei anteriorly as in *Erymnochelys*, *Peltocephalus*, and the *Stereogenys*/*Shweboemys* group of the subtribe Stereogenyina (see character list for discussion). The more restricted conditions have a broad or narrow prootic-pterygoid contact in the anterior part of the cavum pterygoidei that extends the canalis cavernosus more anteriorly. In BMNH R.8440 and the other forms, such as *Erymnochelys*, with a widely open cavum, the prootic and pterygoid do not contact here, and the foramen cavernosum is a foramen in the prootic-quadrate suture, near the foramen nervi facialis.

The fenestra ovale and foramen stapedio-temporale are preserved on both sides but are best seen on the right side of BMNH R.8440. They are similar to those structures in other podocnemidids such as *Podocnemis*.

OPISTHOTIC

**Preservation:** The opisthotic is present on both sides of BMNH R.8440, but the posterolateral edges are eroded away on both. The left one is most complete and seems to lack only a small part of the posterolateral end.

**Contacts:** As in other podocnemidids, the opisthotic in *Mogharemys* contacts the supraoccipital anteromedially, the prootic anteriorly, the quadrate anterolaterally, and the exoccipital posteromedially. A squamosal contact may or may not have been present.

**Structures:** The opisthotic of *Mogharemys* does not appear to enter the edge of the foramen jugulare posterius, which is formed only by the exoccipital. The opisthotic forms the dorsomedial roof of the fenestra postotica. The lateral head vein and stapedial artery apparently extend through the aditus canalis stapedio-temporalis close together and separate anteriorly where the canalis cavernosus lies close to the foramen stapedio-temporale; all presumably related to the large size of the cavum pterygoidei. The processus interfenestralis is covered ventrally by basioccipital and quadrate, and it forms the posterior margin of the fenestra ovalis with the prootic forming the anterior margin, as in all turtles. The opisthotic forms the posterior margin of the foramen jugulare anterius, there is no ossified anterior margin in BMNH R.8440.

BASISPHENOID

**Preservation:** Most of the basisphenoid is present in BMNH R.8440; the anterior edges, including the rostrum basioccipitale, are eroded away as are the finer structures on the dorsal surface. The condylus occipitalis is also broken.

**Contacts on ventral surface:** As in the other podocnemidids, the basisphenoid in *Mogharemys* contacts the pterygoids anterolaterally

(contacts represented only by some sutural edges as the pterygoids here are missing), the basioccipital posteriorly, the prootic laterally, and the quadrate laterally, as in the Podocnemididae and Bothremydidae.

**Structures on ventral surface:** The foramen posterius canalis carotici interni in *Mogharemys* leads into the foramen anterius canalis carotici interni via a very short canalis caroticus internus, all formed by the basisphenoid. *Erymnochelys* has a similar arrangement for the canalis, and the canal and foramina are relatively large in size. The cavum pterygoidei is also relatively large in BMNH R.8440, as in *Erymnochelys*. The basisphenoid forms the ventromedial wall of the cavum, and there is a ventral ridge marking the contact with the pterygoid, now missing.

**Contacts on dorsal surface:** As in the other podocnemidids, in *Mogharemys* the contacts of the basisphenoid are with the pterygoid anterolaterally, the prootic dorsally, and the basioccipital posteriorly. As the rostrum basioccipitale is missing (or not ossified), any more possible anterior contacts are not determinable.

**Structures on dorsal surface:** The rostrum basisphenoidale is probably broken away rather than unossified as the margin is a broken edge. The sella turcica and dorsum sellae are preserved and are similar to *Erymnochelys*. The sulcus cavernosus is essentially absent as the foramen cavernosum opens in the prootic in the dorsolateral roof of the cavum pterygoidei and the cavum and sulcus cavernosus are not differentiated due to the large size of the cavum pterygoidei. There is no processus clinoideus or foramen nervi abducentis (VI) on either side of the dorsum sellae. The foramen nervi abducentis probably is absent, being included in the large anterior opening of the cavum pterygoidei. The processus clinoideus seems to be broken on both sides.

### *Cordichelys*
Figures 52–55

The skull of *Cordichelys* YPM 7457 is particularly well preserved and complete, which makes it convenient to include wider comparisons with other Stereogenyini. The reader should make use of this section as an introduction to Stereogenyini skull morphology in general.

#### PREFRONTAL

**Preservation:** The prefrontals in YPM 7457 (formerly YPM 6205) lack the anterior edges on both sides, and small portions near the maxilla contacts.

**Contacts:** As in the other subtribe Stereogenyina, the contacts are with the other prefrontal on the midline, the maxilla anteroventrolaterally, and the frontal posteriorly.

**Structures:** *Cordichelys* has a shallow interorbital depression, wider and less defined than in *Podocnemis*, that appears to be restricted to this taxon. The interorbital distance in *Cordichelys* is relatively broad, significantly different from *Podocnemis* and agreeing with the other Stereogenyini. The dorsal edges of the orbits are raised in *Cordichelys* and this produces the apparent depression rather than a well-defined groove as in *Podocnemis*.

#### FRONTAL

**Preservation:** Both frontals in YPM 7457 are complete.

**Contacts:** The contacts are with the other frontal on the midline, the prefrontal anteriorly, the postorbital posterolaterally, and the parietal posteriorly, as in the other subtribe Stereogenyina. These general relations of the frontal are found in all Stereogenyini and most pelomedusids, but the frontal of *Bairdemys venezuelensis* is particularly similar in shape to the frontal in *Latentemys*. The interorbital distance is slightly greater in *Cordichelys* than it is in *Shweboemys,* but the distance is nearly the same in *Bairdemys venezuelensis* and *Latentemys*.

**Structures:** *Cordichelys* is slightly convex between the orbits, but it is not curved to the degree seen in *Bairdemys venezuelensis*. In lateral view the prefrontal and frontal of *Bairdemys* are dorsally convex, curving anteroventrally from the fronto-parietal suture. In all other members of the Stereogenyini the skull roof is nearly flat in profile. Among Podocnemidinae only *Podocnemis* approaches the degree of curvature in *Bairdemys venezuelensis* but does not reach it.

The ventral surface of the frontal in *Cordichelys* and other Stereogenyini is dominated by a thick and well-developed parasagittal septum orbitotemporale separating

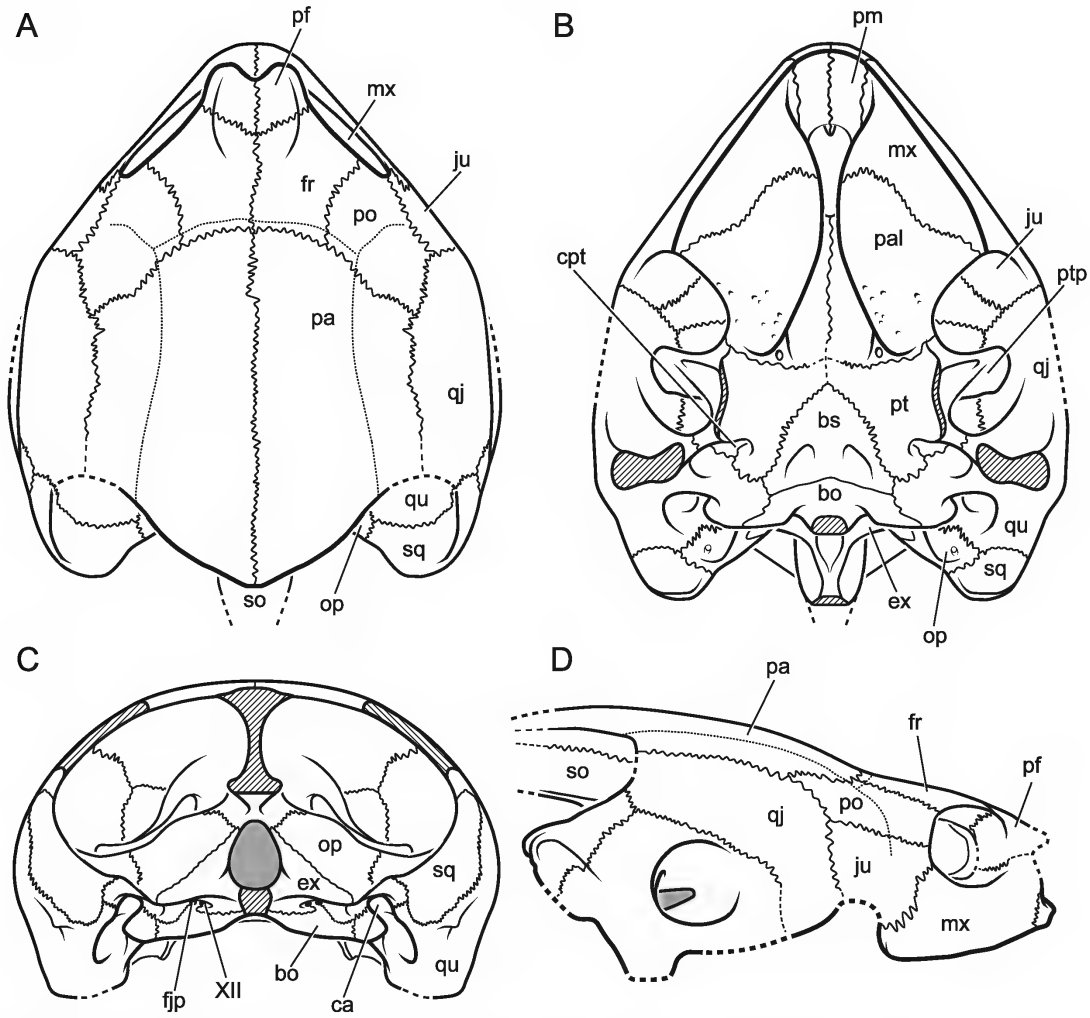



Fig. 52. *Cordichelys antiqua* (Andrews), n. gen. Partially restored skull based on YPM 7457. **A,** dorsal; **B,** ventral; **C,** occipital; **D,** lateral. [F. Ippolito, del.]

the fossa orbitalis laterally from the sulcus olfactorius medially. The septum is lowest anteriorly where it is a continuation of the ridge on the ventral surface of the prefrontal that separates the fossa orbitalis and the fossa nasalis. The ridge on the frontal thickens and deepens posteriorly where it contacts the processus inferior parietalis posteromedially and the posterior wall of the fossa orbitalis posterolaterally. The structure of this region in Stereogenyini differs from other pelomedusoides.

In turtles generally, a view into the front part of the cavum cranii shows a pair of parasagittal walls ending anteriorly in the fissure ethmoidalis. Each wall, the processus inferior parietalis, is formed dorsally by the parietal primarily and by the frontal to a varying extent and ventrally by the pterygoid (Gaffney, 1979). In all pleurodires the processus trochlearis pterygoidei forms a buttress with the palatine and jugal, so that there is a separate postorbital wall, the septum orbitotemporale (Gaffney et al., 2006). Cryptodires lack this structure and usually are open behind the orbit. In pleurodires the connection between the processus trochlearis pterygoidei and the septum orbitotemporale

Fig. 53. *Cordichelys antiqua* (Andrews), n. gen. Partially restored ventral view of skull based on YPM 7457. [F. Ippolito, del.]

is variably developed, being shortest in chelids (Gaffney, 1979: fig. 55) and largest in podocnemidines (Gaffney, 1979: fig. 54). In pelomedusoides this connection forms a parasagittal wall, lateral to the processus inferior parietalis, with a tunnellike space between them. This space, the sulcus palatinopterygoideus (Gaffney et al., 2006), is filled by the pars rostromedialis of the M. pterygoideus (Schumacher, 1973: figs. 9 and 11). In the podocnemidines generally and the Stereogenyini in particular, the wall is extensive and thick, involving the palatine and frontal bones and being thicker and more extensive than the braincase wall itself, which is the processus inferior parietalis. In Stereogenyini when looking into the front part of the cavum cranii, a structure that appears to be the fissure ethmoidalis is visible. However, this structure is not the fissure; rather, it is the anteromedially expanded septum orbitotemporale that connects with the processus

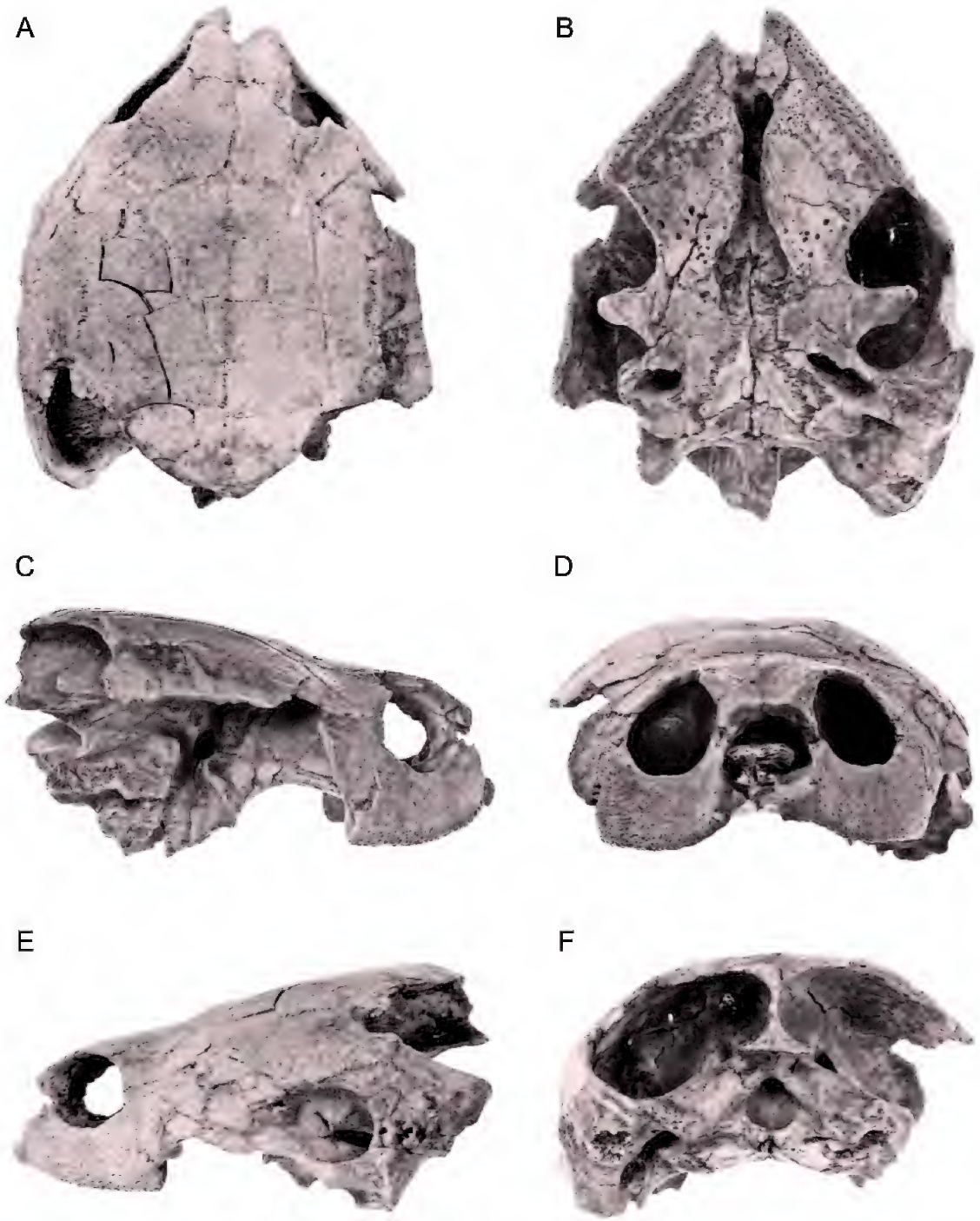



Fig. 54. *Cordichelys antiqua* (Andrews), n. gen. YPM 7457. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [F. Ippolito, del.]

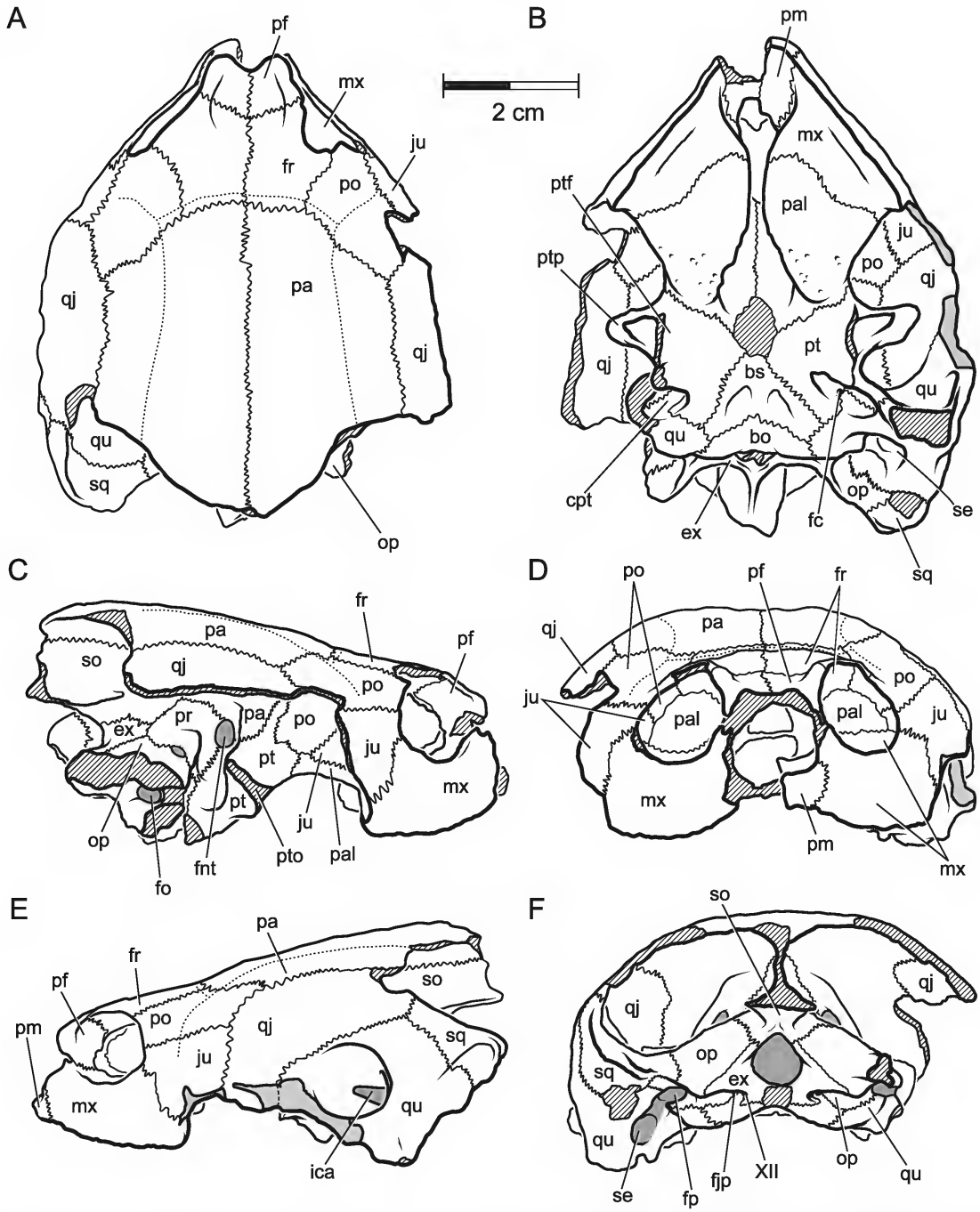



Fig. 55. *Cordichelys antiqua* (Andrews), n. gen. YPM 7457. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [L. Starin, del.]

trochlearis pterygoidei. The fissure ethmoidalis is present but it is posterior to the septum orbitotemporale. The anterior edge of the septum orbitotemporale is formed by the frontal dorsally and the palatine ventrally. More posteriorly it is formed by the pterygoid ventrally and the parietal dorsally (fig. 55C).

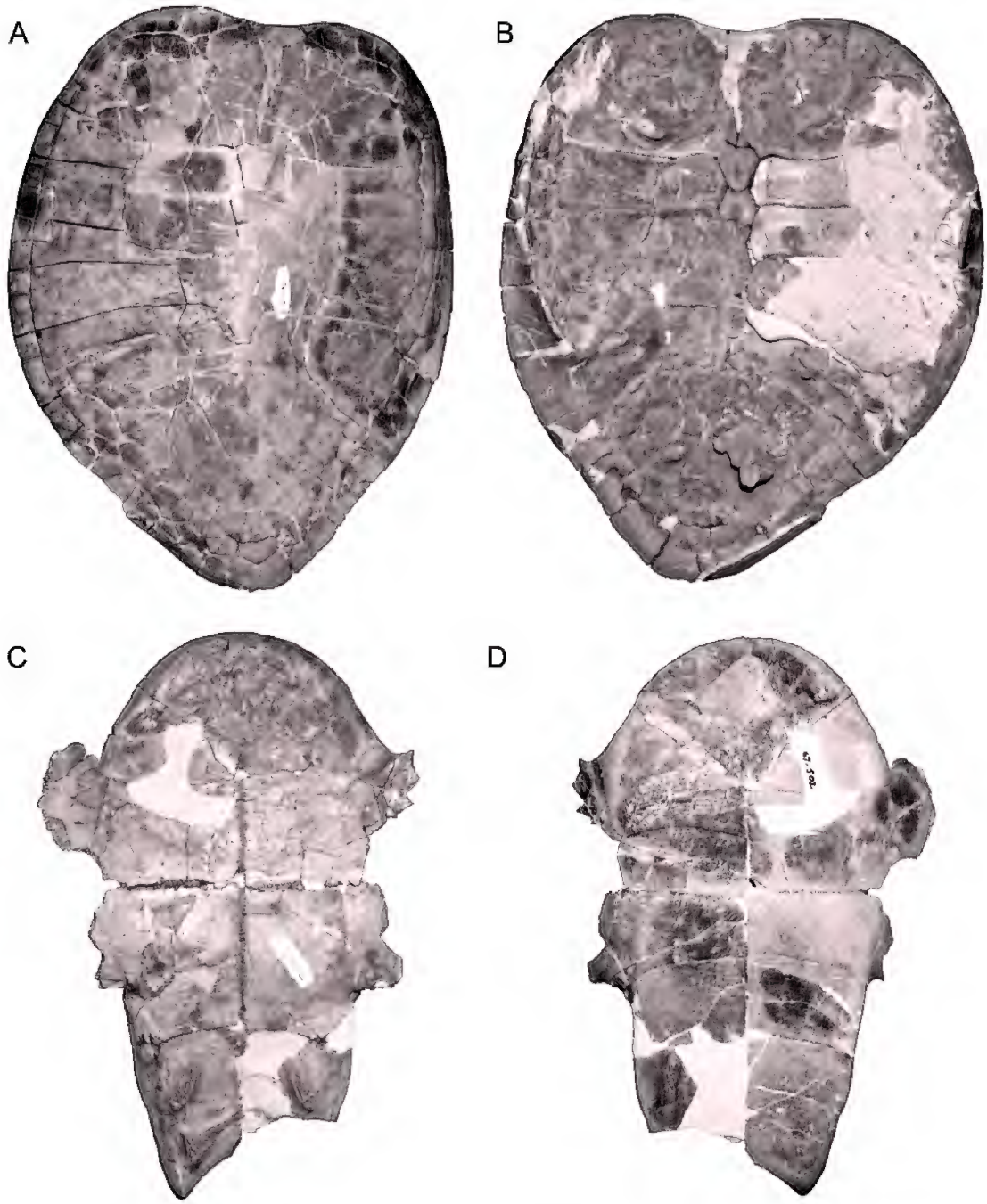



Fig. 56. *Cordichelys antiqua* (Andrews), n. gen. Shell of YPM 7457. **A,** dorsal; **B,** ventral. [E. Gaffney, del.]

The orientation of the orbital rim varies among the subtribe Stereogenyina. In *Cordichelys* the orbit is almost completely vertical with no dorsal component as in *Brontochelys* and *Stereogenys*. The orbit in *Cordichelys* faces anterolaterally, as in most subtribe Stereogenyina.

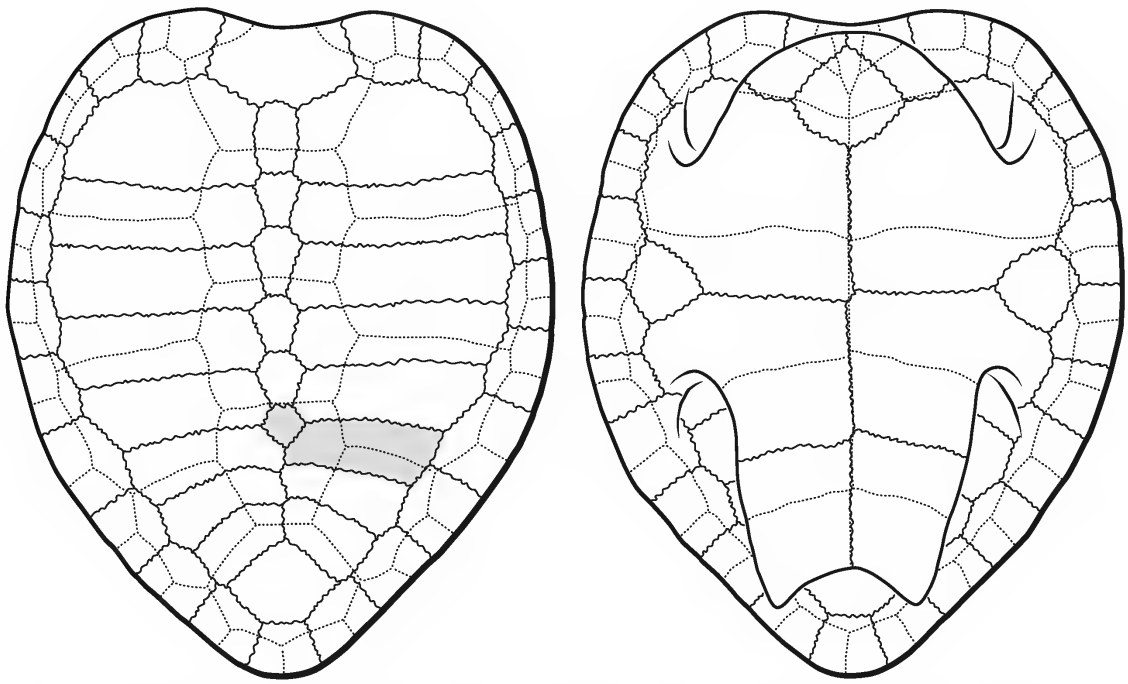


Fig. 57. *Cordichelys antiqua* (Andrews), n. gen. Partially restored shell of YPM 7457. [C. Wilson, del.]

PARIETAL

**Preservation:** The left parietal in YPM 7457 is, as far as can be determined, complete. Only a small piece of the posterior edge is missing from the right parietal.

**Contacts of dorsal plate:** The parietal in *Cordichelys* contacts the parietal on the midline, the frontal anteriorly, the postorbital laterally, and the quadratojugal posterolaterally, as in the other subtribe Stereogenyina in which the temporal roof is known. The parietal in *Bairdemys* differs from that in *Cordichelys* in having a longer contact with the postorbital, but otherwise they agree closely. Only the frontal and part of the postorbital contact areas are preserved in *Brontochelys*, *Shweboemys*, and *Latentemys*. The free plate of the parietal is missing in all these specimens, but the preserved areas agree with *Bairdemys*. In *Stereogenys* (BMNH R.3190) the sutures are not clear, but the bone contacts appear to be the same as in the other Stereogenyini.

**Structures of dorsal plate:** The complete extent of the temporal roof (parietal and quadratojugal) can be determined only in *Cordichelys*, *Bairdemys venezuelensis*, and *Stereogenys* (BMNH R.3190). In these taxa the temporal roof is relatively extensive and comparable in extent and shape to *Peltocephalus* among the living podocnemidids. In these genera the temporal roof completely covers and extends posterior to the otic chamber.

**Contacts of processus inferior parietalis:** This structure is not entirely clear of matrix in YPM 7457, but on the external surface of the right processus inferior parietalis it can be seen that the parietal contacts the palatine anteroventrally and the pterygoid ventrally. The parietal reaches the prootic posteroventrally, and the supraoccipital posteriorly, all as in other podocnemidids.

**Structures of processus inferior parietalis:** The ventral surface of the parietal in all Stereogenyini has a thick parasagittal, ventral ridge, the processus inferior parietalis, that forms the side wall to the cavum cranii. Although not determinable in *Cordichelys*, the cavum cranii in *Bairdemys*, *Stereogenys* (BMNH R.3191, DPC 4120), and *Latentemys*, has distinct cerebral expansions. *Brontochelys* differs from these in having much smaller cerebral expansions as in *Podocnemis*

*expansa*; they are indeterminate in the remaining specimens in the Stereogenyini.

The foramen nervi trigemini in YPM 7457 is formed by the parietal anterodorsally, the prootic dorsolaterally, and the pterygoid ventrally.

JUGAL

**Preservation:** The left jugal in YPM 7457 has a small break on its ventral cheek margin, but is otherwise complete. The right jugal lacks the posterior part of its lateral plate.

**Contacts of lateral plate:** As in *Bairdemys venezuelensis*, the jugal in *Cordichelys* contacts the maxilla anteroventrally, the postorbital dorsally, and the quadratojugal posterodorsally.

**Structures of lateral plate:** The jugal of *Cordichelys* forms the posteroventral margin of the orbit. The degree of exposure in the rim is less than in *Latentemys* and significantly less than in *Bairdemys venezuelensis*.

The degree of cheek emargination in the subtribe Stereogenyina is determinable only in *Bairdemys venezuelensis*, *B. hartsteini*, *Cordichelys*, and *Stereogenys*, the cheek bones being mostly missing in *Latentemys*, *Shweboemys*, and *Brontochelys*. *Stereogenys* has only a very slight emargination, the least of the group. *Cordichelys* lacks most of the right cheek, but much of the ventral margin of the left cheek is a natural edge indicating an emargination greater than *Stereogenys* but less than *Bairdemys venezuelensis* and *B. hartsteini*.

**Contacts and structures of medial process:** In the floor of the fossa orbitalis the jugal in *Cordichelys* contacts the maxilla anteriorly and laterally and the palatine medially. In the posterior view of the septum orbitotemporale, the jugal contacts the postorbital dorsally and the palatine ventrally. In contrast to the other subtribe Stereogenyina, the jugal in *Cordichelys* does not reach the pterygoid here due to a contact of the postorbital and palatine. The jugal forms part of the septum orbitotemporale as in the other subtribe Stereogenyina and does not enter the triturating surface.

QUADRATOJUGAL

**Preservation:** In YPM 7457 the left quadratojugal lacks only part of the ventral margin, but enough of the natural edge remains to show the original emargination. The right quadratojugal lacks its entire ventral margin.

**Contacts:** The quadratojugal in *Cordichelys* contacts the parietal medially, the quadrate posteroventrally, the squamosal posterodorsally, the postorbital anterodorsally, and the jugal anteroventrally, as in *Bairdemys venezuelensis*.

**Structures:** Above and posterior to the quadrate, a thin process of the quadratojugal contacts the squamosal. In these contacts *Cordichelys* agrees closely with *Bairdemys* but not with *Podocnemis*, which has a very small postorbital and lacks a quadratojugal-postorbital contact. As in nearly all other turtles the quadratojugal of *Cordichelys* has a curved contact with the quadrate paralleling the cavum tympani margin. The quadratojugal and the jugal form most of the edge of the cheek emargination in podocnemidids.

SQUAMOSAL

**Preservation:** The left squamosal in YPM 7457 is nearly complete, lacking only some abraded area posteriorly. The right squamosal is entirely missing.

**Contacts:** The squamosal in *Cordichelys* contacts the quadrate anteriorly and ventrally, the opisthotic medially, and the quadratojugal anterodorsolaterally, as in *Bairdemys venezuelensis*.

**Structures:** As in all other turtles the squamosal of *Cordichelys* lies on the posterodorsal margin of the quadrate. It has a narrow contact with the quadratojugal anteriorly and forms the posterolateral margin of the temporal emargination.

In all turtles the squamosal is the primary bone forming the antrum postoticum, which is a space behind and above the cavum tympani. In pelomedusids (*Pelusios* and *Pelomedusa*), the antrum postoticum is relatively large, as in nearly all other turtles. But other pelomedusoides have a variably reduced, antrum postoticum. In most podocnemidids the antrum is smaller than in *Pelusios* but still a distinct space filling the posterior projection of the squamosal. The antrum postoticum is preserved only in *Bairdemys*, *Cordichelys*, *Latentemys*, and *Stereogenys* among the Stereogenyini. The

entire squamosal is absent in *Brontochelys* and *Shweboemys*. In *Cordichelys* and *Latentemys* the antrum postoticum is a distinct, tubular space, much smaller than the *Pelusios* condition and somewhat smaller than in *Podocnemis*. In *Bairdemys* and *Stereogenys*, however, the antrum is reduced to a slit, formed primarily by the quadrate internally and enclosed by the cone-shaped squamosal. The slit is orientated dorsolaterally ventromedially, in common with the plane of the widest dimension in *Latentemys*. Both *Bairdemys venezuelensis* and *B. hartsteini* have the collapsed, slitlike antrum postoticum. Many bothremydids also have a small or absent antrum, but in this group the space is either a small canal and not a slit or completely filled with bone.

POSTORBITAL

**Preservation:** The postorbital in YPM 7457 is present on both sides. The right one is complete; the left one lacks only a small part of the ventral margin.

**Contacts of lateral plate:** The postorbital in *Cordichelys* contacts the frontal anteromedially, the jugal ventrally, the quadratojugal posteriorly, and the parietal posteromedially, as in *Bairdemys*.

**Structures of lateral plate:** The postorbital forms the posterodorsal orbital margin, as in *Bairdemys*.

**Contacts of medial process:** In the anterior surface of the septum orbitotemporale, facing the fossa orbitalis, the postorbital contacts the frontal dorsomedially, the palatine medially, and the jugal ventrally. In the posterior surface of the septum orbitotemporale, facing fossa temporalis, the postorbital contacts the parietal dorsomedially, the pterygoid ventromedially, the jugal ventrolaterally, and the palatine ventrally.

**Structures of medial process:** The postorbital in *Cordichelys* as in other subtribe Stereogenyina forms part of the roof and lateral wall of the sulcus palatinopterygoideus and part of both surfaces of the septum orbitotemporale.

PREMAXILLA

**Preservation:** In YPM 7457 the left premaxilla is preserved completely, the right one is missing much of its anterior and medial parts.

**Contacts:** The premaxilla in *Cordichelys* contacts the maxilla posterolaterally and the other premaxilla medially on the midline.

**Structures:** The premaxilla is an important element in the distinctive triturating surface morphology characteristic of the Stereogenyini. All the members of this group have a secondary palate that is formed primarily from the maxilla and palatine. The premaxilla forms the anteromedial part of the triturating surface and the labial ridge that is the edge of the triturating surface. In *Cordichelys* the premaxillary surface forms a ventrally opening concavity on the midline, very similar to the one seen in *Bairdemys venezuelensis*. *Shweboemys* also has a median premaxillary depression, but it is shallower and smoothly continuous with the posterolateral or maxillary surface of the triturating area. Although the available material of *Stereogenys* is not well preserved, two specimens, BMNH R.1390 and a cast of CGM 10027 (cast is AMNH 14736), show a premaxillary depression similar to *Bairdemys venezuelensis* and *Cordichelys* in being deep and well defined but unique in having a small accessory ridge on the premaxilla. This ridge parallels the labial ridge and is separated from it by a narrow groove; the ridge is entirely limited to the premaxilla and is continuous across the midline.

The premaxilla in the Stereogenyini forms the anterior margin of the palatal cleft (missing in *Brontochelys* and *Latentemys*). The margin is a C-shaped trough, opening posteriorly. In *Podocnemis* and *Dacquemys* the maxillae meet behind the premaxillae, but in the other vomerless podocnemidids the premaxillae are free posteriorly as in the Stereogenyini.

The premaxillary portion of the snout shows varying degrees of protrusion or "pinching" among the Stereogenyini. *Stereogenys* shows the most protruded, with the labial margin of the skull being concave anterolaterally. *Bairdemys hartsteini* is also pinched and protruded while *Shweboemys*, *Cordichelys*, and *Latentemys* are slightly protruded but not pinched. *Brontochelys* seems to be lacking a protrusion (although the premaxillae are absent and the anterior part of the skull is broad). *Bairdemys venezuelensis* lacks pinching and a protrusion.

Wood (1970) characterized "*Shweboemys*" (here *Brontochelys*) *gaffneyi* as having a horizontal midline labial ridge and *Shweboemys pilgrimi* and "*Shweboemys*" (here *Cordichelys*) *antiqua* as being notched on the midline in anterior view. Unfortunately, the two Asian species are represented by specimens that are broken in this area, but it does seem likely that at least *Shweboemys* has a premaxillary notch or embayment similar to that seen in *Bairdemys hartsteini*. *Bairdemys venezuelensis* lacks a notch. *Cordichelys* also has an embayment similar to that in *Bairdemys hartsteini*, and the partially preserved specimens of *Stereogenys* also seem consistent with a notch. In *Latentemys* the notch is not determinable. Thus, only *Brontochelys* and *Bairdemys venezuelensis* seem to be lacking a premaxillary embayment, but even this is not definitely determinable in *Brontochelys*. *Podocnemis* and many other podocnemidids have a midline protrusion or overhanging projection rather than a notch. *Mogharemys* is missing the premaxillae and lacks this area. However, the basal podocnemidid *Lapparentemys* has a midline notch and that may be the primitive condition.

Laterally, the premaxilla of *Cordichelys* is longer and lower than the premaxilla in *Bairdemys venezuelensis*; this is presumably related to the shorter and deeper preorbital region of *Bairdemys*.

Dorsally, the premaxilla forms the ventral and part of the lateral margin of the aperture narium externa. The oval aperture is similar in shape in both *Bairdemys* and *Cordichelys*, the Stereogenyini that have the margins best preserved. *Stereogenys* and *Shweboemys* are damaged in this area, but show what appear to be broader narial openings. The other taxa are indeterminate.

In *Cordichelys* and *Bairdemys venezuelensis* there is a median, anteroposteriorly oriented ridge on the dorsal surface of the premaxilla that begins at the anteroventral margin of the aperture narium externa and rises in height along the floor of the fossa nasalis. There is a similar ridge in *Podocnemis*.

MAXILLA

**Preservation:** In YPM 7457 both maxillae are nearly complete; there is some damage around the prefrontal suture.

**Contacts of vertical plate:** The maxilla of *Cordichelys* contacts the premaxilla anteromedially, the jugal posterodorsally, and the prefrontal anterodorsally, as in the other subtribe Stereogenyina.

**Structures of vertical plate:** The width of the facial portion of the skull expressed in the angle of the labial ridge to the midline can be used to differentiate a broader jawed group from a narrower jawed group. In *Bairdemys venezuelensis* the angle is 45°, in *Cordichelys* it is 40° and in *Latentemys* it is 30°. In *Brontochelys*, the labial ridge angle is about 60°. In *Shweboemys* it is hard to be sure due to damage, but the angle is around 50°–55°. In *Stereogenys* 50° seems to be the most reliable. *Mogharemys* is too broken along the labial ridge to make a measurement, but the preserved triturating morphology is most similar to the broad jawed *Brontochelys*. The taxa with labial ridge angles of 50° or more might be interpreted as constituting a broad-jawed group and those with labial ridges of 45° or less a narrow-jawed group. But the variation of the angles really forms more of a spectrum and the recognition of groups is somewhat arbitrary.

**Contacts of horizontal plate:** The maxilla in *Cordichelys* contacts the premaxilla anteromedially, the palatine posteromedially, and the jugal posterolaterally, as in the other subtribe Stereogenyina. As far as can be determined, the maxillae do not meet on the midline in any of the subtribe Stereogenyina.

**Structures of horizontal plate:** The labial ridge forms the outermost part of the triturating surface. In *Bairdemys*, *Cordichelys*, and *Latentemys,* the labial ridge is relatively deep and narrow. These are in contrast to the labial ridge of *Stereogenys,* which is lower and thicker. In *Brontochelys* and *Shweboemys* the labial ridge is largely worn away, but the preserved parts are more consistent with a low and thick labial ridge.

The Stereogenyini has as its principal synapomorphy, a well-developed secondary palate. Secondary palates occur in a number of other turtles groups, with *Osteopygis* and *Rhetechelys* (Gaffney, 1979) having the most extensive ones. The Stereogenyini, however, differ from all other turtles with secondary palates in having a midline cleft extending from the premaxillae posteriorly to the

choanal opening proper. Was this cleft covered with soft tissue in life? Did the cleft provide an opening for air or other material? Did it mean that these turtles were warm-blooded?

The maxilla in the Stereogenyini forms the anterolateral part of the palate and the palatine forms the posterior part. The maxilla-palatine suture trends laterally from the midline then curves posterolaterally until it reaches the jugal in the margin of the fenestra temporalis inferior.

In *Cordichelys* and some other subtribe Stereogenyina, the maxillary part of the triturating surface has a distinct swelling or convexity just lateral to the midline cleft and internal to the labial ridge. This convexity is part of a raised platform that (in ventral view) is stepped above the palatine portion of the palate. The maxilla-palatine suture in *Bairdemys* intersects part of the convexity, but for the most part it lies close to the demarcation between the anterolateral raised section and the more posterior lower section. *Latentemys* agrees with *Bairdemys venezuelensis* and also has a raised convexity. *Cordichelys* has a similar palatal morphology, but the maxilla-palatine suture runs more anteriorly through part of the convexity. *Brontochelys*, *Shweboemys*, and *Stereogenys* have much flatter, triturating surfaces; there is a gentle curve to the surface, but no raised convexity is present.

PALATINE

**Preservation:** Both palatines in YPM 7457 are apparently complete. It is possible that a small part of the thin bone on the midline is missing.

**Contacts:** In ventral view the palatine of *Cordichelys* contacts the maxilla anterolaterally, the other palatine medially on the midline, and the pterygoid posteriorly. It is possible that there was a basisphenoid contact, but the medial edges of the pterygoids are damaged. On the dorsal surface, the palatine dorsal process contacts the frontal anterodorsally and the parietal dorsally. In the anterior wall of the septum orbitotemporale, the palatine contacts the maxilla anterolaterally, the jugal laterally, the postorbital posterolaterally, and the frontal dorsally.

The figure of "*Shweboemys*" (now *Cordichelys*) *antiqua* in Gaffney (1979: fig. 136) that shows a basisphenoid-palatine contact is incorrect. Although this area is damaged in this specimen, further work has shown that the pterygoids meet in the midline.

**Structures:** The palatine in the subtribe Stereogenyina has a horizontal plate forming the posterior portion of the secondary palate ventrally, a vertical plate extending dorsally to contact the parietal, and a horizontal plate meeting on the midline to form the primary palate. The presumed primitive condition of the palatine in turtles in general and podocnemidids in particular is a flat, platelike bone forming the roof of the palate, the posterior margin of the apertura narium interna, and a small anterolateral contribution to the triturating surface (posteromedial to the maxilla). This condition can be seen in *Euraxemys* (Gaffney et al., 2006). In the Stereogenyini, the palatine shows two modifications from this primitive condition: a secondary palatal plate ventral to the primary palatal palate and a vertical process extending dorsal to the primary palate and reaching the temporal roofing bones.

The variation in length of the secondary palate is mostly dependent on the palatine length and the degree of palatine participation. Within the Stereogenyini there is a range of variation in length of the secondary palate from *Stereogenys*, which has the longest secondary palate, to *Bairdemys venezuelensis*, which has the shortest. Here we use a comparison based on the ratio of total skull length to secondary palate length, as expressed by the length of the midline cleft. These measurements are not exact due to variation in preservation and positions of measurements, but the ratio does seem the most objective way to compare the secondary palate in these skulls. The ratios of secondary palate lengths to skull lengths seem to fall into three categories. *Stereogenys* is alone with its palate about 40% of the skull length. *Cordichelys*, *Shweboemys*, and *Brontochelys* have palates that are about 30% of skull length, although there is a certain amount of spread, and the two Asian species are not well preserved. *Brontochelys* completely lacks premaxillae making both measurements only approximate. *Bairdemys venezuelensis* and

*Latentemys* are in the 20% range, although *Latentemys* must be considered problematical due to significant missing areas of the palate.

There could be a small foramen palatinum posterius in *Cordichelys* at the posteriormost end of the secondary palate, just under the fold of bone and not visible in ventral view.

QUADRATE

**Preservation:** The right quadrate in YPM 7457 is missing, except for the contact area around the prootic and opisthotic, but the left one is nearly complete, lacking some of the condylus mandibularis and some of the ventral edge.

**Contacts on lateral surface:** In *Cordichelys* the quadrate contacts the quadratojugal anterodorsally and the squamosal posterodorsally, as in *Bairdemys*.

**Structures on lateral surface:** YPM 7457 is one of the few subtribe Stereogenyina skulls to show a complete cheek and its emargination is somewhat less than in *Bairdemys venezuelensis*. The quadratojugal in *Cordichelys* is more extensive ventrally, although the ventral edge of the quadrate could be broken and more like that in *Bairdemys*.

The cavum tympani in *Cordichelys* is shallower than that in *Bairdemys venezuelensis,* but both have a closed incisura columellae auris enclosing the eustachian tube as in all the other subtribe Stereogenyina. The eustachian tube sulcus that opens on the posterior surface of the occiput in *Cordichelys* is open, communicating with the fenestra postotica, in contrast to the closed condition, separating the two structures seen in *Bairdemys*. There is no fossa precolumellaris. The antrum postoticum in *Cordichelys* is relatively small compared to pelomedusids, but it is not a narrow slit as seen in *Bairdemys venezuelensis*.

**Contacts on dorsal and anterior surface:** As in the other podocnemidids, the quadrate in *Cordichelys* contacts the prootic anteromedially, the opisthotic posteromedially, and the squamosal posteriorly and posterolaterally.

**Structures on dorsal and anterior surface:** The foramen stapedio-temporale is in its usual position for podocnemidids, between the quadrate and prootic facing more dorsally than anteriorly.

**Contacts on ventral surface:** As in *Bairdemys*, the contacts in *Cordichelys* are with the pterygoid anteromedially, the basisphenoid medially, the basioccipital posteromedially, and the prootic medially, within the cavum pterygoidei.

**Structures on ventral surface:** The condylus mandibularis in *Cordichelys* is in about the same relative position as it is in *Bairdemys venezuelensis*. The cavum pterygoidei in *Cordichelys* is also similar in position and extent to that in *Bairdemys venezuelensis*, except that the ventral opening is in a slightly more horizontal plane in *Cordichelys*. The quadrate shows on both sides the opening of the cavum cavernosus, formed between the quadrate, pterygoid, and prootic.

**Contacts on posterior surface:** The quadrate contacts in *Cordichelys* are with the squamosal dorsolaterally, the opisthotic dorsomedially, and the basioccipital ventromedially.

**Structures on posterior surface:** The fenestra postotica in *Cordichelys* is confluent with the sulcus eustachii in contrast to *Bairdemys*. The left quadrate shows a foramen chorda tympani inferius just below the sulcus eustachii.

PTERYGOID

**Preservation:** In YPM 7457 the pterygoids are present on both sides and nearly complete. They lack some of the margins of the cavum pterygoidei. Most of the pterygoid flange is broken off on both sides, but a significant portion of its base remains on the right pterygoid.

**Contacts on ventral surface:** The pterygoid in *Cordichelys* contacts the palatine anteriorly, the basisphenoid posteromedially, the prootic posteriorly in the cavum pterygoidei, and the quadrate posterolaterally. The possible medial contact of the pterygoids, which would prevent a palatine-basisphenoid contact, is not determinable in YPM 7457 because the thin medial edges of both pterygoids are abraded away, revealing the overlying basisphenoid. As preserved, there is no midline contact of the pterygoids. There is also a median contact of the palatines with the basisphenoid. However, this area is eroded and these contacts seem to be artifacts of preservation. It is most likely that the

pterygoids were worn away and that a narrow midline, pterygoid contact separating the palatines from the basisphenoid was present as in *Bairdemys*.

**Structures on ventral surface:** The processus trochlearis pterygoidei in *Cordichelys* lies at a right angle to the midline as in the other subtribe Stereogenyina. The cavum pterygoidei is formed ventrally by the pterygoid as in the other podocnemidids. The base of a well-developed pterygoid flange is present on the ventral surface of the left pterygoid.

**Contacts on dorsal surface:** In *Cordichelys* the contacts at the base of the processus trochlearis pterygoidei (the septum orbitotemporale posterior surface) are with the postorbital dorsolaterally, the palatine anteroventrally, and the parietal anterolaterally. Due to the postorbital-palatine contact there is no pterygoid-jugal contact in *Cordichelys*. The contacts of the crista pterygoidea are not visible internally, but externally they are the usual contacts in pleurodires: the parietal anterodorsally and the prootic posterodorsally.

**Structures on dorsal surface:** The pterygoid in *Cordichelys* forms the anteroventral margin of the foramen nervi trigemini, the parietal the anterodorsal margin, and the prootic the posterodorsal margin, as in the other podocnemidids.

SUPRAOCCIPITAL

**Preservation:** Most of the supraoccipital is present in YPM 7457, but the posterior edge is a broken margin, so its original extent may have been longer as in *Bairdemys*.

**Contacts:** The contacts are as in *Bairdemys*.

**Structures:** The crista supraoccipitalis in *Cordichelys* has a relatively wide, horizontal plate, on the ventral edge of the crista, as in *Bairdemys*.

EXOCCIPITAL

**Preservation:** Both exoccipitals in YPM 7457 are present and complete except for parts of the condylus occipitalis. Enough bone is present, however, to show that the exoccipitals did make up at least part of the condylus, along with the basioccipital.

**Contacts:** As in *Bairdemys*.

**Structures:** The two foramen nervi hypoglossi are recessed and united in a single opening on the occipital surface, as in most of the other subtribe Stereogenyina except *Bairdemys sanchezi*. The foramen jugulare posterius is completely closed as in other subtribe Stereogenyina. The condylus occipitalis does not retain any original surface, but the exposed elements indicate that it was made up of the basioccipital as well as the two exoccipitals, as in all other subtribe Stereogenyina. The fenestra postotica is closed, and separated from the sulcus eustachii, also as in *Bairdemys*.

BASIOCCIPITAL

**Preservation:** The basioccipital in YPM 7457 is cracked on the midline, but it lacks only part of the condylus occipitalis surface.

**Contacts:** As in *Bairdemys venezuelensis* and *B. hartsteini*.

**Structures:** As in *Bairdemys*, except that *Cordichelys* has a flat, slightly concave ventral surface to the basioccipital; *Bairdemys venezuelensis* has a convexity on the midline.

PROOTIC

**Preservation:** Both prootics are preserved intact in YPM 7457.

**Contacts:** As in *Bairdemys venezuelensis* and *B. hartsteini*.

**Structures:** As in *Bairdemys venezuelensis* and *B. hartsteini*.

OPISTHOTIC

**Preservation:** Both opisthotics are preserved intact in YPM 7457.

**Contacts:** As in *Bairdemys venezuelensis* and *B. hartsteini*.

**Structures:** As in *Bairdemys venezuelensis* and *B. hartsteini*.

BASISPHENOID

**Preservation:** The basisphenoid in YPM 7457 is complete, but the area of palatine and pterygoid underlying it anteriorly is abraded, exposing areas the basisphenoid that had been covered.

**Contacts on ventral surface:** The contacts in *Cordichelys* appear to be the same as in *Bairdemys venezuelensis*. The anterior contacts of the basisphenoid, whether or not it reached the palatines, however, are unclear due to the breakage of both palatines and pterygoids. The contacts could easily be the same as in *Bairdemys venezuelensis*, however.

**Structures on ventral surface:** The basisphenoid in *Cordichelys* is incompletely clear of matrix inside the cavum pterygoidei, and the foramen posterius canalis carotici interni cannot be seen.

**Contacts and structures on dorsal surface:** The dorsal surface of YPM 7457 is not visible.

*Latentemys*
Figures 58–61

PREFRONTAL

**Preservation:** The anterior margins of both prefrontals in BMNH R.11998 are broken edges.

**Contacts:** As in *Bairdemys venezuelensis.*

**Structures:** The prefrontal in *Latentemys* is flat, not convex as in *Bairdemys venezuelensis.* There is no midline depression as in *Cordichelys.*

FRONTAL

**Preservation:** Both frontals are complete in BMNH R.11998.

**Contacts:** As in *Bairdemys venezuelensis:* the frontal on the midline, the prefrontal anteriorly, the postorbital posterolaterally, the parietal posteriorly, and on the ventral surface, the palatine posteroventrally.

**Structures:** The frontal in *Latentemys* borders the orbit as in *Bairdemys venezuelensis*, and it sends a process posteroventrally to contact the dorsal process of the palatine, also as in other subtribe Stereogenyina.

PARIETAL

**Preservation:** The parietals in BMNH R.11998 are missing all the dorsal plates except those directly over the cavum cranii. None of the original posterior or lateral margins are preserved.

**Contacts and structures of dorsal plate:** As preserved, the only contacts in BMNH R.11998 are with the other parietal medially, the frontal anteriorly, and the postorbital anterolaterally.

**Contacts and structures of processus inferior parietalis:** The anterior margin of the processus is broken away in BMNH R.11998, but what is present agrees with *Brontochelys.* It contacts the palatine anteroventrally, the pterygoid ventrally, the prootic posteroventrally, and the supraoccipital posteriorly. As in other podocnemidids, the foramen nervi trigemini in *Latentemys* is formed by the parietal, prootic and pterygoid.

JUGAL

**Preservation:** On the left side of BMNH R.11998 the jugal is complete internally and is missing only the posterior part of the lateral plate externally. The right jugal lacks the lateral plate and the dorsal part of the medial process.

**Contacts and structures of lateral plate:** As preserved, the jugal in *Latentemys* contacts the maxilla anteroventrally and the postorbital dorsally. The jugal forms the posteroventral part of the orbital rim, as in the other subtribe Stereogenyina.

**Contacts of medial process:** In the anterior wall of the septum orbitotemporale and the floor of the fossa orbitalis, the jugal contacts the maxilla anteriorly and laterally, the palatine medially, and the postorbital posterodorsally, as in *Cordichelys.* In the septum orbitotemporale posterior wall, the jugal contacts the postorbital dorsomedially, the palatine ventromedially, and the pterygoid posteriorly in a relatively short suture.

**Structures of medial process:** The medial process of the jugal in *Latentemys* does not reach the triturating surface, and it forms the ventral portion of the septum orbitotemporale, as in most of the other subtribe Stereogenyina.

QUADRATOJUGAL

The quadratojugal is not preserved in BMNH R.11998.

SQUAMOSAL

**Preservation:** The squamosal in BMNH R.11998 is preserved on both sides, but only the conical posterior part is present, and the anterior contacts with cheek elements is missing.

**Contacts and structures:** As in other subtribe Stereogenyina, the squamosal in *Latentemys* contacts the quadrate anteromedially and the opisthotic medially. As in other subtribe Stereogenyina, the squamosal is a cone-shaped bone fitting around antrum postoticum of quadrate. It is similar to that bone in *Bairdemys*, but lacks the ventral flange seen in that taxon, agreeing with *Cordichelys.*

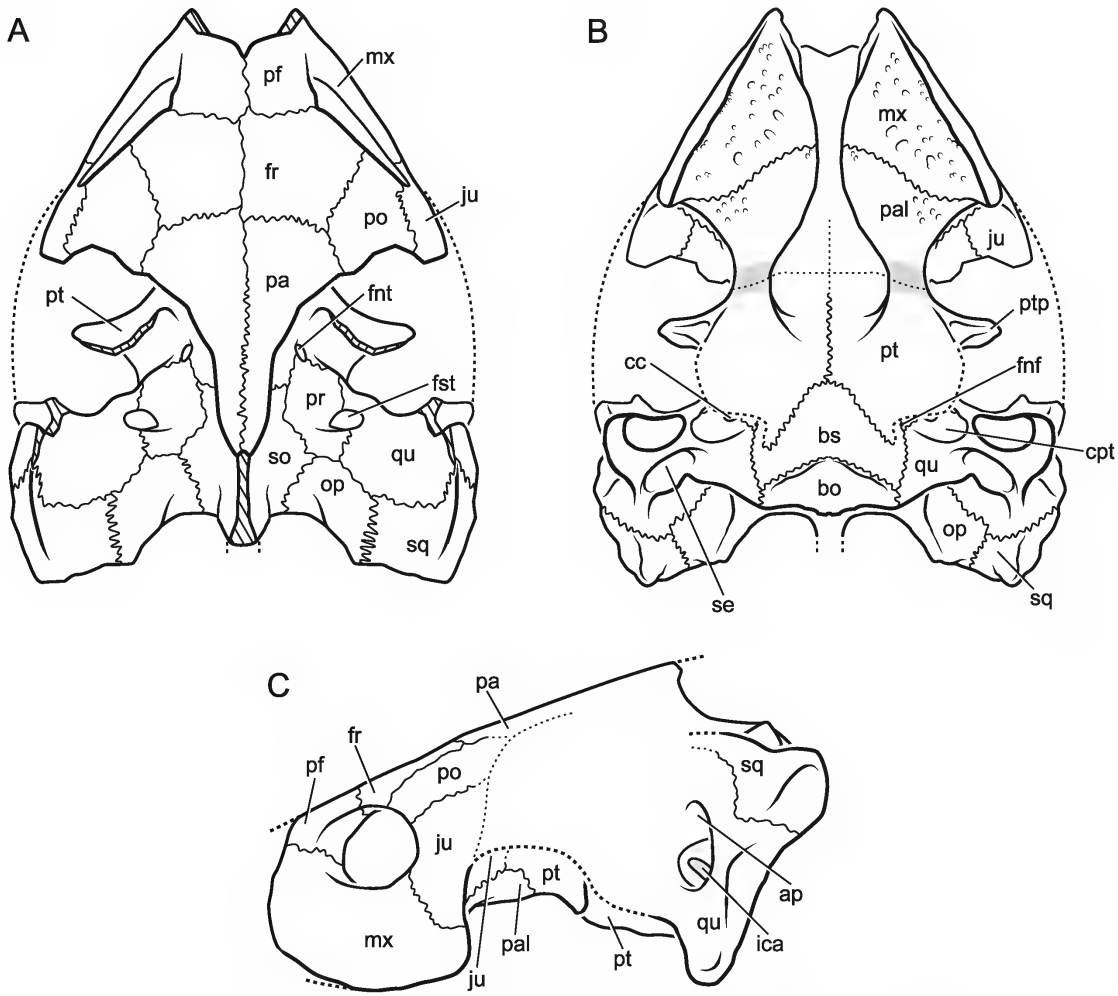



Fig. 58. *Latentemys plowdeni,* n. gen. et sp. Partially restored skull based on BMNH R.11998. **A,** dorsal; **B,** ventral; **C,** lateral. [C. Wilson, del.]

POSTORBITAL

**Preservation:** The postorbital is preserved on both sides of BMNH R.11998. On the right side only the most medial part of the medial process is preserved in the orbit, on the left side all of the medial part and some of the lateral plate is preserved, but the posterior part of the lateral plate is missing.

**Contacts and structures of lateral plate:** As preserved, the postorbital in *Latentemys* contacts the frontal anteromedially and the jugal ventrally. It forms the posterodorsal part of the orbital rim.

**Contacts of medial process:** In the anterior surface of the septum orbitotemporale the postorbital of *Latentemys* contacts the frontal dorsomedially, the palatine ventrally, and the jugal ventrolaterally. In the posterior surface of the septum orbitotemporale, the postorbital contacts the parietal dorsomedially, the pterygoid ventromedially, and the jugal ventrolaterally.

**Structures of medial process:** The postorbital forms the dorsal part of the septum orbitotemporale and part of the roof and lateral wall of the sulcus palatinopterygoideus.

PREMAXILLA

The premaxilla is not preserved in BMNH R.11998.

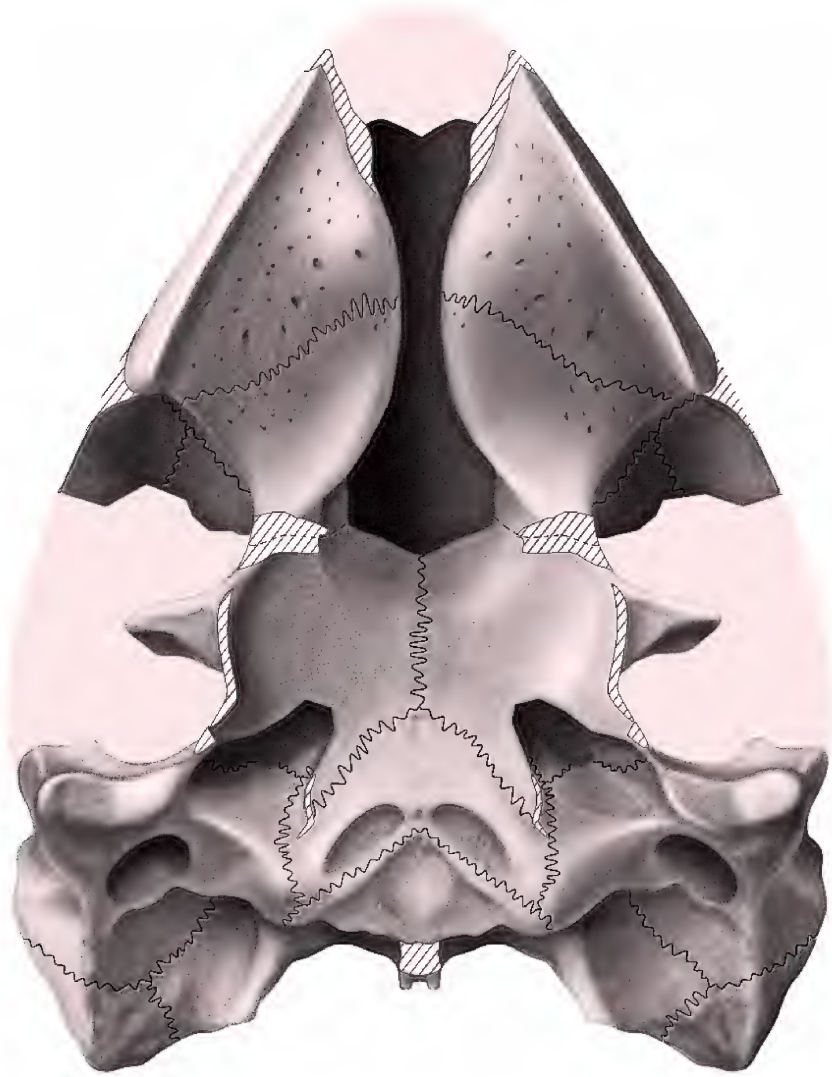


Fig. 59. *Latentemys plowdeni,* n. gen. et sp. Partially restored ventral view based on BMNH R.11998. [C. Wilson, del.]

MAXILLA

**Preservation:** Both maxillae are preserved in BMNH R.11998. Both appear to be complete. They may lack a small portion along the premaxilla contact.

**Contacts of vertical plate:** As in *Bairdemys venezuelensis*, except for the premaxilla contact, which is unknown.

**Structures of vertical plate:** The part of the orbital margin and choanal passages formed by the maxilla in *Latentemys* is very similar to those areas in *Cordichelys.*

**Contacts of horizontal plate:** As preserved, the maxilla in *Latentemys* contacts the palatine posteromedially and the jugal posterolaterally.

**Structures of horizontal plate:** The labial ridge is high and narrow as in *Bairdemys*. The large ventral convexity characteristic of *Bairdemys venezuelensis* is represented in *Latentemys* by a shallow convexity as in *Cordichelys.*

PALATINE

**Preservation:** The palatine in *Latentemys* is preserved in BMNH R.11998 on both sides.

Both are missing most of the posterior contact with the pterygoids and the left one has some of the anteromedial edge broken.

**Contacts:** As in *Bairdemys venezuelensis*, on the ventral surface the palatine in *Latentemys* contacts the maxilla anterolaterally, the other palatine medially on midline above the secondary palate, and the pterygoid posteriorly. On the dorsal surface the palatine contacts the frontal anterodorsally. In the fossa orbitalis, the palatine contacts the maxilla anterolaterally, the jugal laterally, the postorbital posterolaterally, and the frontal dorsomedially.

**Structures on dorsal surface:** The palatine in *Latentemys* forms much of the floor of the fossa orbitalis, the posteroventral margin of the foramen orbito-nasale, and the anterior floor of sulcus palatinopterygoideus. The foramen palatinum posterius could possibly be a small hole just under the posterior end of the secondary palate, near the pterygoid suture.

**Structures on ventral surface:** The palatine in *Latentemys* forms less than half of the posterior triturating surface secondary palate, in contrast to *Bairdemys venezuelensis* in which the palatine forms at least half of the palate and is wider than in *Latentemys*. The medial edge of the median cleft in *Latentemys* is curved as in *Bairdemys* and *Cordichelys*.

QUADRATE

**Preservation:** The quadrates in BMNH R.11998 lack their anterior cheek portions and the anterior part of the cavum tympani, but the medial and ventral portions are present on both sides.

**Contacts on lateral surface:** As preserved, the only contact is with the squamosal posterodorsally.

**Structures on lateral surface:** The posterior portion of the cavum tympani in *Latentemys* shows a closed incisura columellae auris containing stapes and eustachian tube that is separated posteriorly from the fenestra postotica as in *Bairdemys* but in contrast to the other subtribe Stereogenyina. The fossa precolumellaris is not preserved. The antrum postoticum in *Latentemys* is small, as in *Cordichelys*, but not flattened and nearly absent as in *Bairdemys*.

**Contacts and structures on dorsal and anterior surface:** As in *Bairdemys venezuelensis* and *Cordichelys*.

**Contacts on ventral surface:** Most of the contacts in *Latentemys* are as in *Bairdemys*, with the basisphenoid medially, the basioccipital posteromedially, and the prootic medially, within the cavum pterygoidei. But the cavum pterygoidei in *Latentemys* is comparatively larger than in most of the other subtribe Stereogenyina, so that the pterygoid and quadrate are separated medially by the basisphenoid, although they contact on the lateral side of the cavum pterygoidei.

**Structures on ventral surface:** The condylus mandibularis in *Latentemys* is in about the same relative position as it is in *Bairdemys venezuelensis*. The cavum pterygoidei in *Latentemys* is also similar in position and orientation to that in *Cordichelys*, but relatively larger. Both quadrates show the opening of the cavum cavernosus, formed between the quadrate, pterygoid, and prootic.

**Contacts on posterior surface:** As in *Bairdemys venezuelensis*.

**Structures on posterior surface:** The fenestra postotica in *Latentemys* is separated by bone from the sulcus eustachii, in contrast to all other subtribe Stereogenyina, except *Bairdemys*.

PTERYGOID

**Preservation:** Both pterygoids in BMNH R.11998 are present but damaged to some extent. The anterior margins of both are broken edges except on the left side. The right processus trochlearis pterygoidei and both pterygoid flanges are missing and the posterior floor of the cavum pterygoidei is broken away on both sides.

**Contacts on ventral surface:** The contacts are with the palatine anteriorly, the basisphenoid posteromedially, and the quadrate posterolaterally. The midline contact with the other pterygoid is long in *Latentemys*, longer than in *Bairdemys* and *Cordichelys*.

**Structures on ventral surface:** The left processus trochlearis pterygoidei is present in BMNH R.11998 and is at right angles to the midline as in other subtribe Stereogenyina. There is a small concavity on the

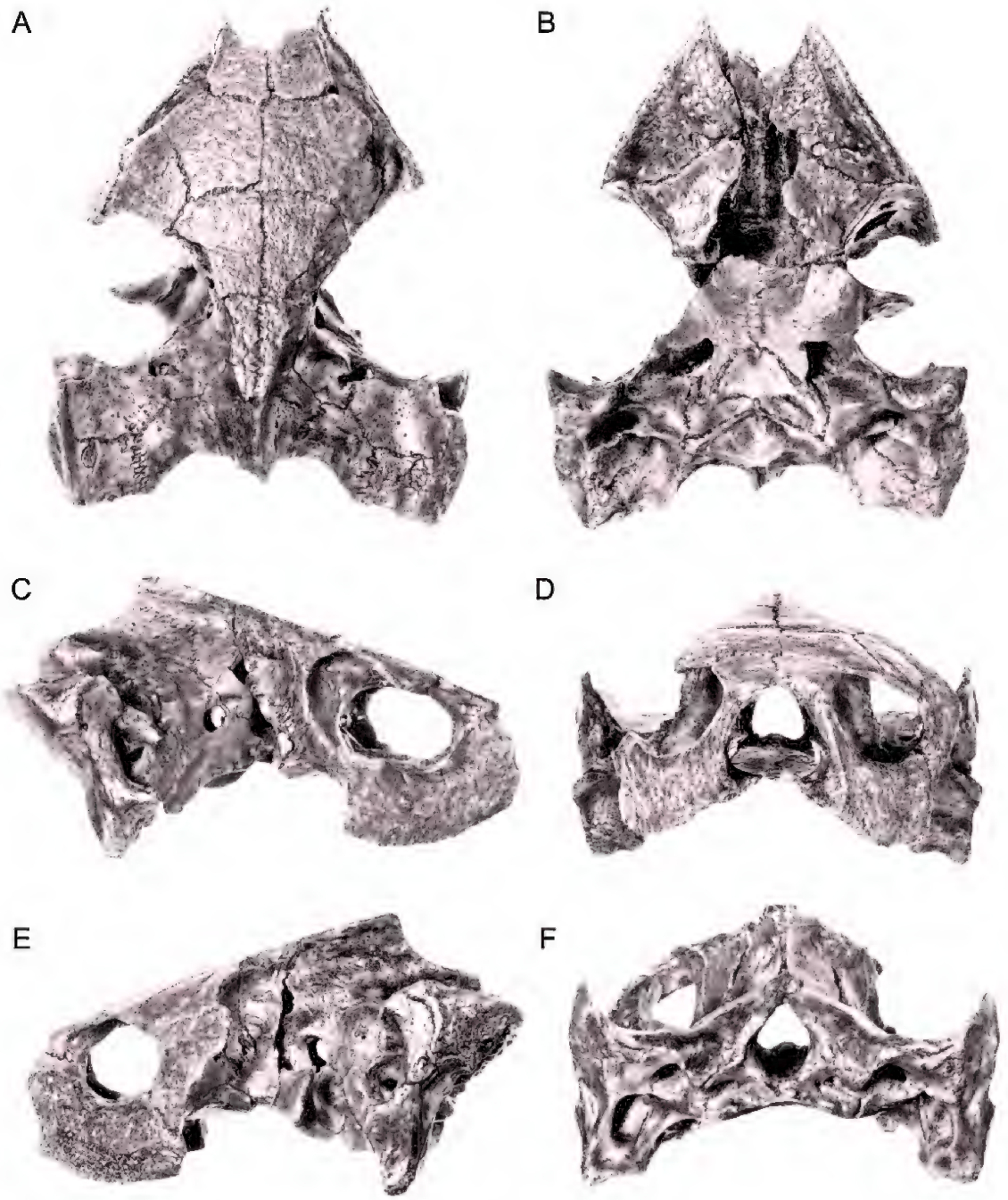



Fig. 60. *Latentemys plowdeni,* n. gen. et sp. BMNH R.11998. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [G. Giardina, del.]

ventral side of the base of the processus in *Latentemys*, as in other subtribe Stereogenyina. The cavum pterygoidei is mostly visible due to the breakage of some of the pterygoid that floors it. The foramen cavernosum lies in the dorsal roof of the cavum pterygoidei as in other subtribe Stereogenyina and is formed laterally by the ptery-

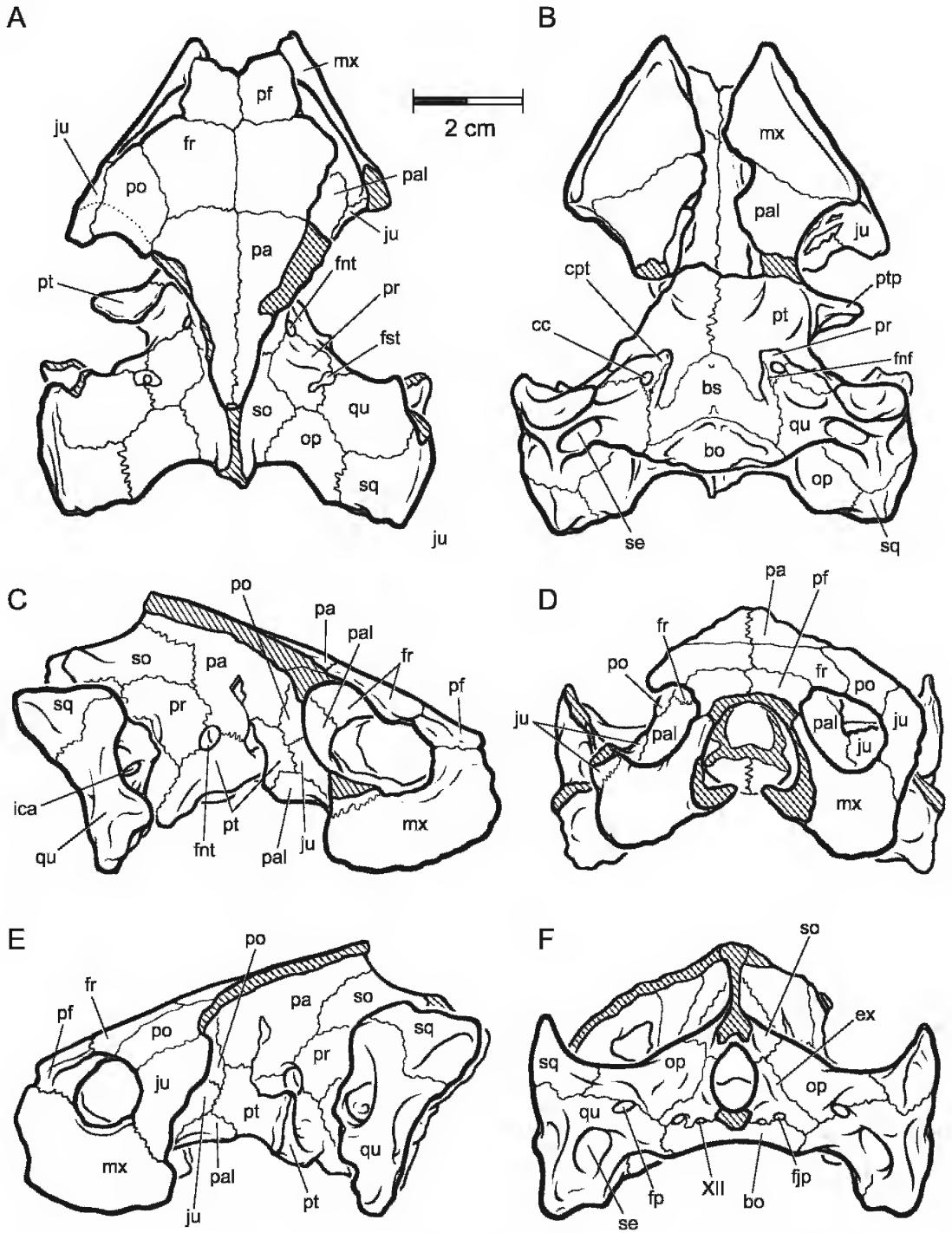



Fig. 61. *Latentemys plowdeni,* n. gen. et sp. BMNH R.11998. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [E. Heck, del.]

goid. The prootic appears to form its anterior margin and the quadrate its medial margin, as in *Cordichelys*. The pterygoid flange is broken away including its base on the right side, but some of the base remains on the left.

**Contacts and structures on dorsal surface:** On the posterior surface of the septum orbitotemporale in *Latentemys*, the pterygoid contacts the postorbital anterodorsally, the jugal anteroventrally, the palatine ventrally, and the parietal anterodorsally. Most of the crista pterygoidea is broken away in BMNH R.11998, the contacts with the parietal dorsally and the prootic posterodorsally are preserved. The sulcus palatinopterygoideus is formed by the pterygoid laterally, but most of that structure is broken away in BMNH R.11998. The foramen nervi trigemini is formed by the usual elements in *Latentemys*, the pterygoid ventrally, the parietal anterodorsally, and the prootic posterodorsally. On both sides the pterygoid forms what appears to be the foramen nervi vidiani just lateral to the rostrum basisphenoidale and in the floor of the sulcus cavernosus.

SUPRAOCCIPITAL

**Preservation:** In BMNH R.11998 all but the anterior part of the supraoccipital is broken away.

**Contacts and structures:** As in *Bairdemys venezuelensis* and other subtribe Stereogenyina, the supraoccipital in *Latentemys* contacts the parietal dorsally and anteriorly, the prootic anterolaterally, the opisthotic posterolaterally, and the exoccipital posteroventrally. The crista supraoccipitalis is not preserved.

EXOCCIPITAL

**Preservation:** In BMNH R.11998 both exoccipitals are present and complete.

**Contacts:** As in *Bairdemys venezuelensis*.

**Structures:** The condylus occipitalis in *Latentemys* is broken but appears to have been formed by both exoccipitals and the basioccipital. The foramen nervi hypoglossi is recessed and the two foramina medially join to form one distally. The foramen jugulare posterius is closed and separated from the fenestra postotica by a relatively long exoccipital contact (with itself, as is usually the case in turtles, oddly enough).

BASIOCCIPITAL

**Preservation:** In BMNH R.11998 the basioccipital is complete except for a small part of the condylus occipitalis.

**Contacts and structures:** As in *Cordichelys*.

PROOTIC

**Preservation:** In BMNH R.11998 both prootics are present and complete. They are both free of matrix and visible internally as well as externally.

**Contacts and structures:** As in *Cordichelys*.

OPISTHOTIC

**Preservation:** In BMNH R.11998 both opisthotics are present and complete except for some erosion on the distalmost edges.

**Contacts and structures:** As in *Cordichelys* and *Bairdemys venezuelensis* and *B. hartsteini*.

BASISPHENOID

**Preservation:** In BMNH R.11998 the basisphenoid is complete and free of matrix internally and externally.

**Contacts on ventral surface:** The basisphenoid in *Latentemys* contacts the pterygoids anterolaterally, the basioccipital posteriorly, the prootic dorsally inside the cavum pterygoidei, and the quadrate laterally.

**Structures on ventral surface:** The basisphenoid in *Latentemys* forms the lateral walls to the cavum pterygoidei and, anteriorly, the foramen posterius canalis carotici interni that leads, by means of a short canalis caroticus internus, to the foramen anterius canalis carotici interni. The cavum pterygoidei in *Latentemys* is relatively larger than in other subtribe Stereogenyina, not by means of an extension laterally into the quadrate as in *Mogharemys*, but by having a larger diameter. The basisphenoid in *Latentemys* is relatively short in comparison to *Bairdemys* and *Cordichelys*, so that there is a long pterygoid contact anteriorly.

**Contacts on dorsal surface:** The dorsal contacts in *Latentemys*, not usually seen, are with the pterygoid anterolaterally, the prootic laterally, presumably with some part of the palatines anteriorly, but not preserved in BMNH R.11998, and the basioccipital posteriorly.

**Structures on dorsal surface:** The rostrum basisphenoidale in *Latentemys* is a solid rod with the trabeculae fused but not extending

anteriorly, defining the sella turcica posteriorly and medially between the paired trabeculae. The rostrum basisphenoidale in *Latentemys* is shorter than in *Brontochelys*, *Peltocephalus*, *Erymnochelys*, and *Podocnemis*. There is the usual sulcus cavernosus lateral to the trabeculae defining the sella turcica, but as the foramen cavernosum is in the dorsal roof of the cavum pterygoidei, it is not clear what the path of the lateral head vein would be.

The dorsum sellae in *Latentemys* is a prominent, overhanging shelf, lying over the posterior end of the sella turcica, in contrast to the very low dorsum seen in *Brontochelys*. The foramen anterius canalis carotici interni lies at each posterolateral end of the sella turcica beneath the dorsum sellae, as in most *Podocnemis,* but in contrast to *Brontochelys* in which the low dorsum exposes the foramen anterius canalis carotici interni dorsally. The paired processus clinoideus may have been present premortem but the position is now a broken surface. The position of the foramen nervi abducentis (VI) is not clear.

*Brontochelys*
Figures 62–66

PREFRONTAL

**Preservation:** The snout of BMNH R.8570 is eroded and damaged to some extent, so only part of the right prefrontal is preserved.

**Contacts:** As preserved, the prefrontal of BMNH R.8570 contacts the maxilla anteroventrally and the frontal posteriorly.

**Structures:** The prefrontal in BMNH R.8570 forms the anterodorsal margin of the orbit, which in *Brontochelys* faces forward to an unusual degree compared with other subtribe Stereogenyina. There appears to be no remaining natural margins of the apertura narium externa. There may have been a prefrontal anterior extension as seen in *Bairdemys*, as this area is damaged in most of the subtribe Stereogenyina specimens. None of the subtribe Stereogenyina taxa have a broad ventral process of the prefrontal, so the narrow nature of it in BMNH R.8570 is probably accurate.

FRONTAL

**Preservation:** Both frontals are present and complete except for their anterior areas. The left one has a broken margin from the midline to its contact with the postorbital and the right one, although more complete and retaining its prefrontal contact, also has breakage along the orbital margin. The internal areas seem intact.

**Contacts:** In dorsal view the frontal in BMNH R.8570 contacts the other frontal on the midline, the prefrontal anteriorly, the postorbital posterolaterally, and the parietal posteriorly. On its ventral surface the frontal also contacts the dorsal process of the palatine along the medial edge of the septum orbitotemporale, as in other subtribe Stereogenyina.

**Structures:** The frontal forms the dorsal edge of the orbital margin as in the other subtribe Stereogenyina. The orbital margins are damaged in BMNH R.8570, but it seems likely that their orientation is correct. They were probably increased in size due to postmortem damage. On the ventral surface the frontal sends a stout process ventrally to meet the dorsal process of the palatine, forming the medial edge for the septum orbitotemporale, as in the other subtribe Stereogenyina. The space between the two frontal-palatine contacts is wider in *Brontochelys* than in *Lemurchelys*, *Cordichelys* and *Latentemys*, and probably *Stereogenys* (based on the endocast).

PARIETAL

**Preservation:** The parietals in BMNH R.8570 lack all the skull roofing portions, the area directly over the braincase is preserved and the internal parietal areas are preserved.

**Contacts and structures of dorsal plate:** As preserved, the parietal in *Brontochelys* contacts the frontal anteriorly, the other parietal medially, and the postorbital anterolaterally. None of the skull roof overlying the fossa temporalis remains.

**Contacts and structures of processus inferior parietalis:** The parietal in *Brontochelys* contacts the frontal ventral process anteriorly, the pterygoid ventrally, the prootic posteroventrally, and the supraoccipital posteriorly. There does not seem to be a palatine contact. Lateral to the processus inferior parietalis in pleurodires is the septum orbitotemporale, which has the

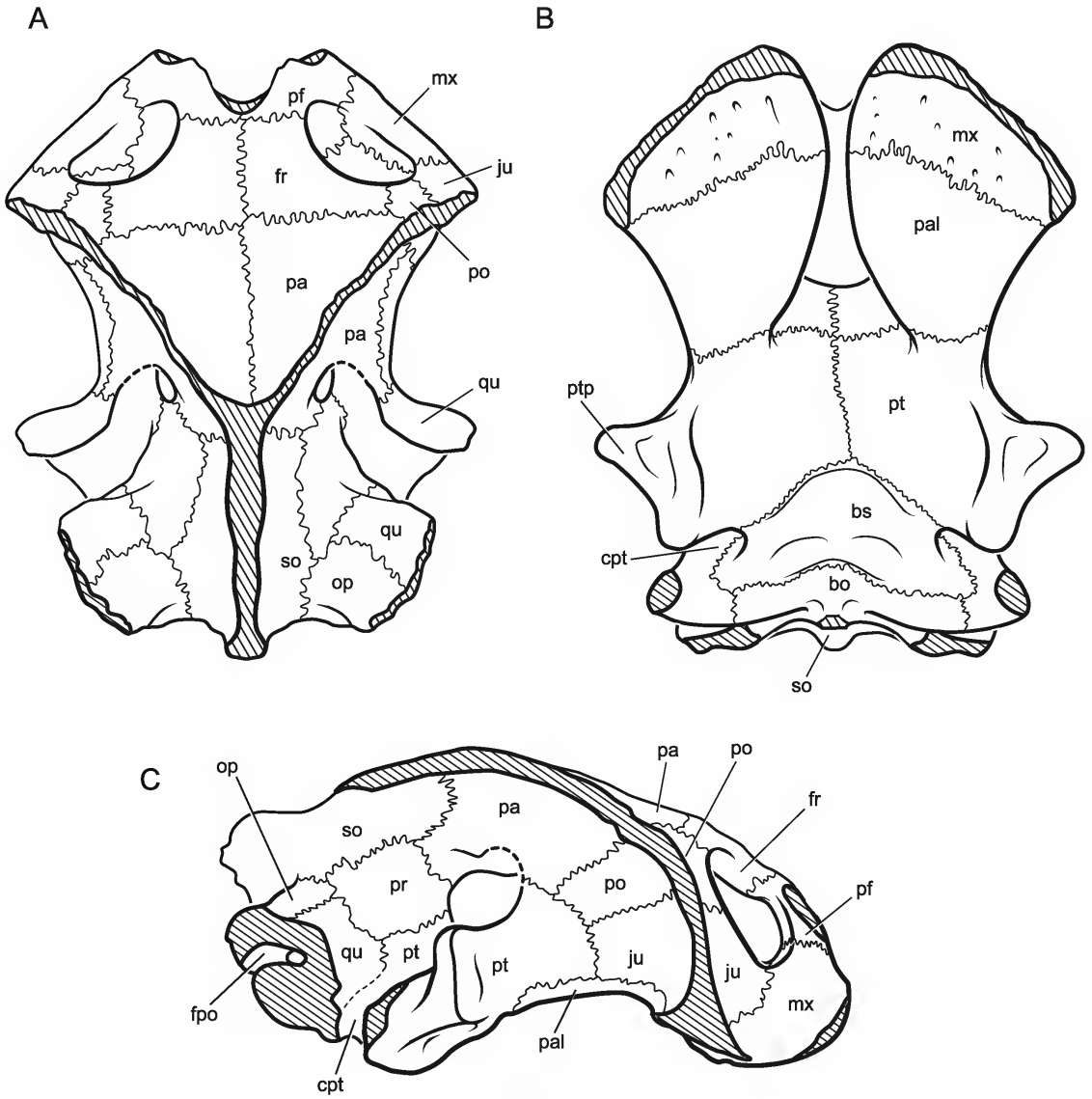



Fig. 62. *Brontochelys gaffneyi* (Wood), n. gen. Partially restored skull based on BMNH R.8570. **A,** dorsal; **B,** ventral; **C,** lateral. [E.E. Nixon, del.]

parietal forming the roof anterodorsally and the lateral wall. The foramen nervi trigemini in *Brontochelys* is formed by the parietal anterodorsally, the prootic dorsolaterally, and, probably, the pterygoid ventrally, although the latter is broken away on both sides.

**Septum orbitotemporale:** The ventral surface of the frontal in *Brontochelys* and other Stereogenyini is dominated by a thick and well-developed parasagittal ridge, the septum orbitotemporale, separating the fossa orbitalis laterally from the sulcus olfactorius medially. This ridge is lowest anteriorly, where it is a continuation of the ridge on the ventral surface of the prefrontal that separates the fossa orbitalis and the fossa nasalis. The ridge on the frontal thickens and deepens posteriorly, where it contacts the processus inferior parietalis posteromedially and the posterior wall of the fossa orbitalis posterolaterally.

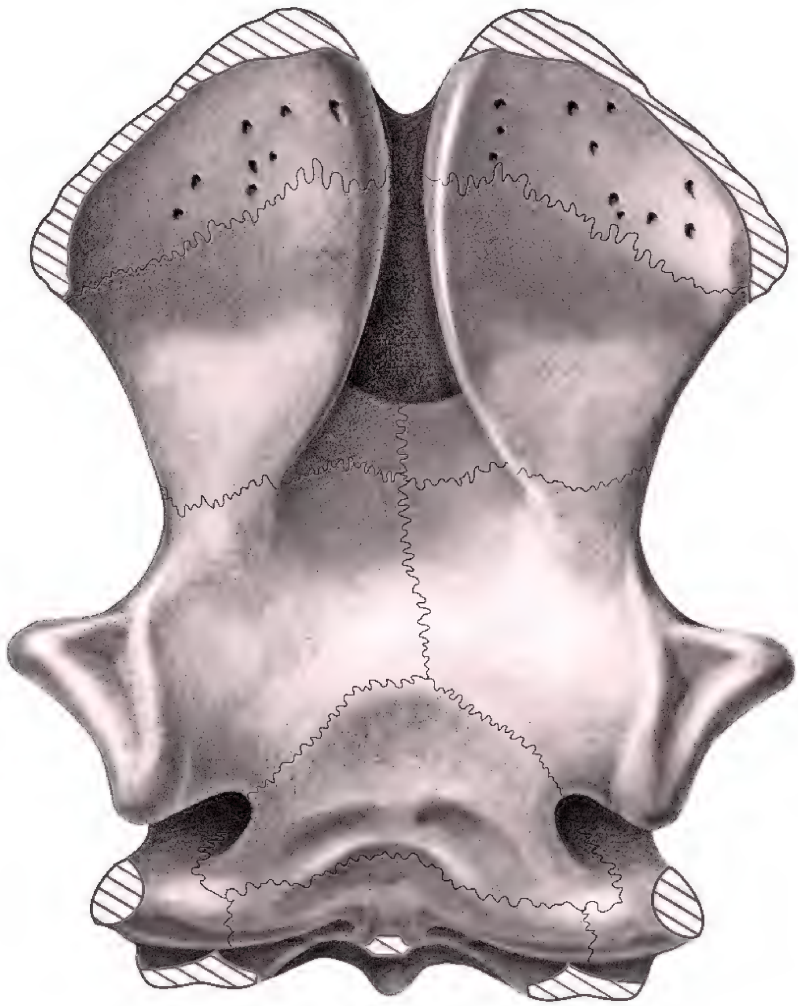


Fig. 63. *Brontochelys gaffneyi* (Wood), n. gen. Partially restored ventral view of skull based on BMNH R.8570. [E.E. Nixon, del.]

JUGAL

**Preservation:** The jugal on both sides of BMNH R.8570 retains the medial process and the orbital part of the lateral plate, but the cheek areas are missing and some of the surface has been eroded on both sides.

**Contacts and structures of lateral plate:** The contacts preserved in *Brontochelys* are with the maxilla anteroventrally, and the postorbital dorsally. There is no indication of the extent of the cheek bones. The jugal forms the ventrolateral part of the orbital rim.

**Contacts and structures of medial process:** In the orbital floor, the jugal in *Brontochelys* contacts the maxilla anteriorly and laterally and the palatine medially. In the septum orbitotemporale (posterior view), the jugal contacts the postorbital dorsomedially, the palatine ventromedially, the pterygoid posteriorly, and the maxilla ventrally, all as in such subtribe Stereogenyina as *Latentemys*. Also as in other subtribe Stereogenyina, the jugal does not form part of the triturating surface.

QUADRATOJUGAL

The quadratojugal is not preserved in BMNH R.8570.

SQUAMOSAL

The squamosal is not preserved in BMNH R.8570.

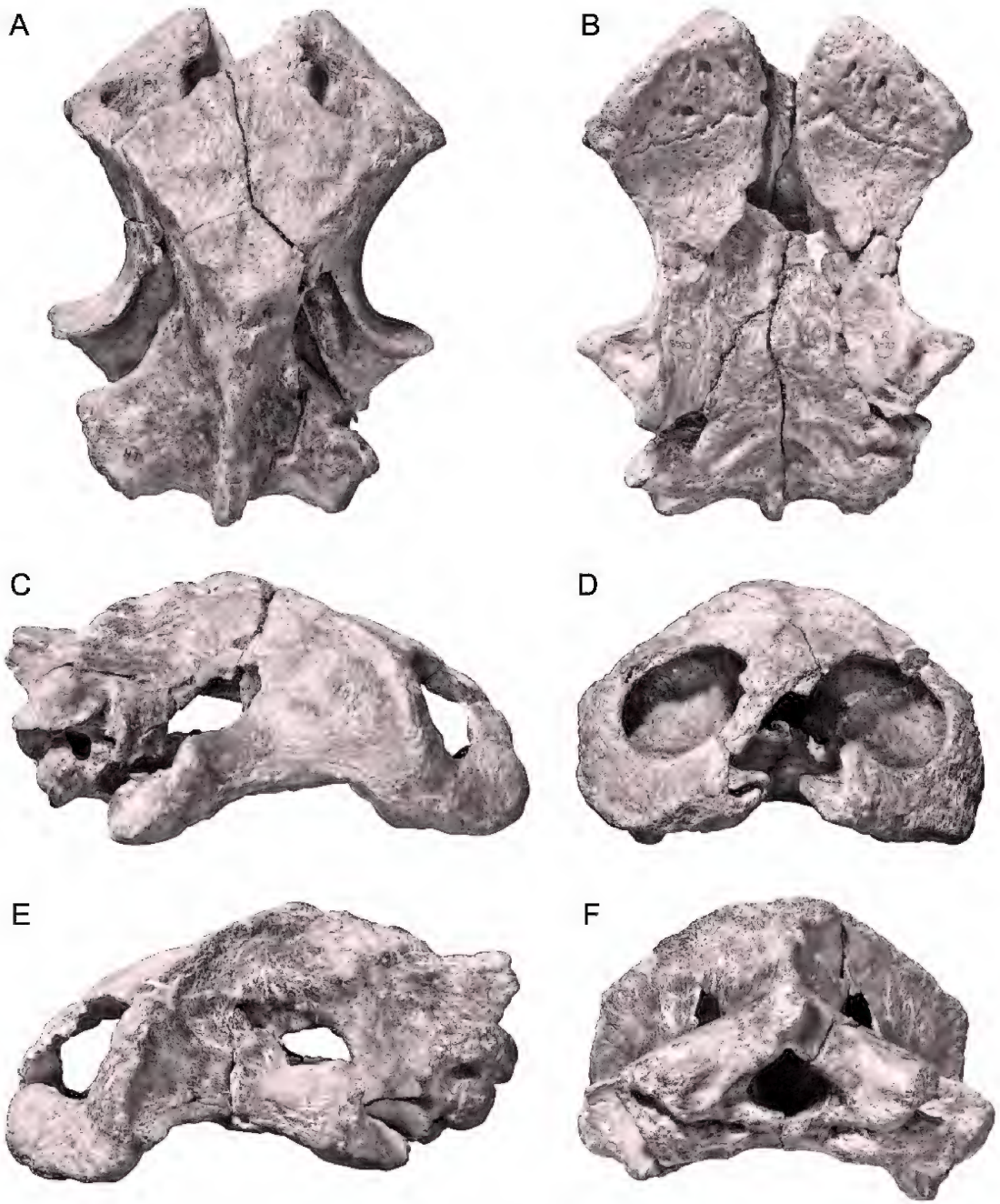



Fig. 64. *Brontochelys gaffneyi* (Wood), n. gen. BMNH R.8570. Skull. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [E.E. Nixon, del.]

POSTORBITAL

**Preservation:** The postorbital in BMNH R.8570 lacks the lateral plate on both sides, but the medial process is present on both sides.

**Contacts and structures of lateral plate:** In *Brontochelys* the contacts are with the frontal anteromedially, the jugal ventrally, and the parietal posteromedially. The postorbital

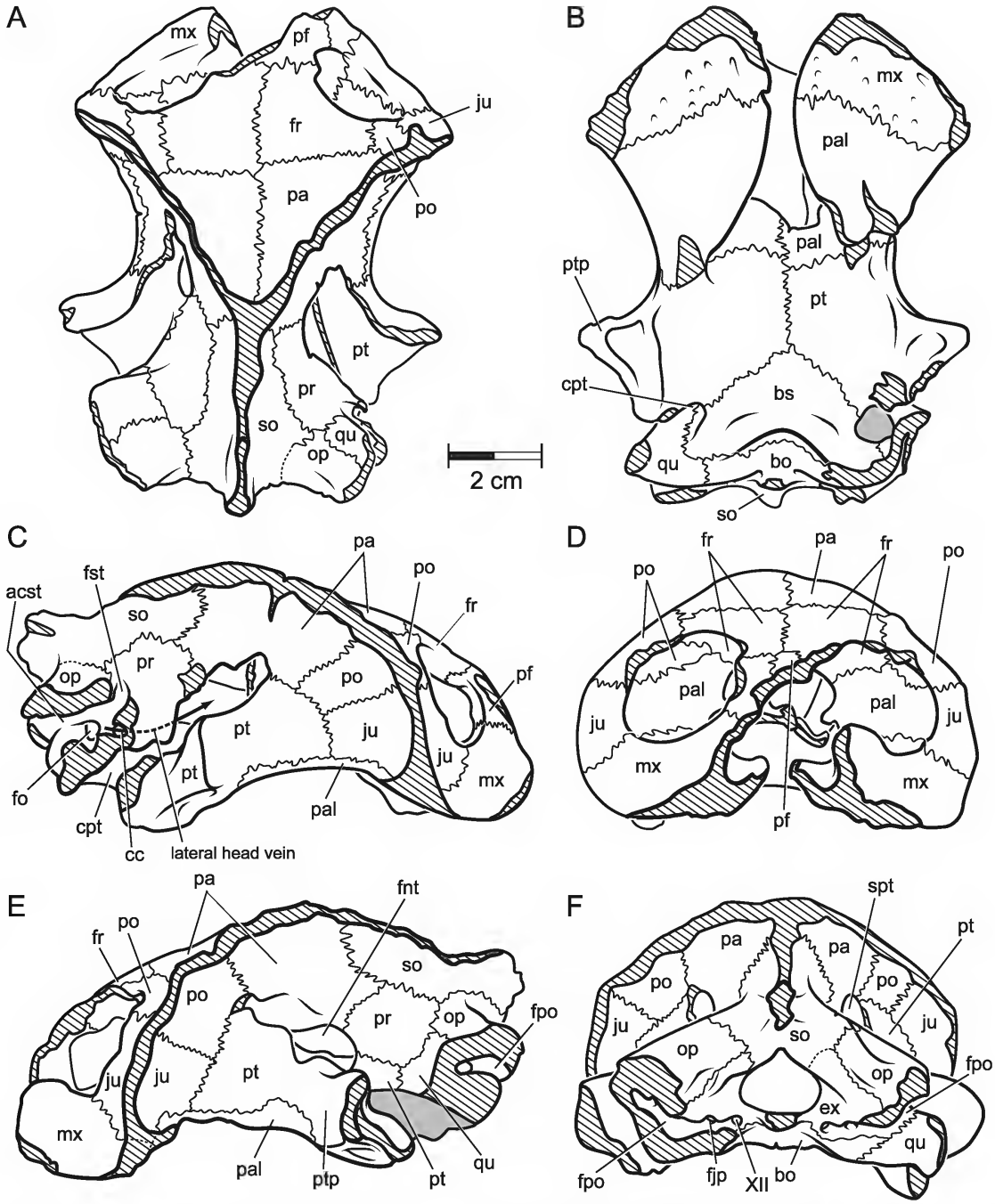
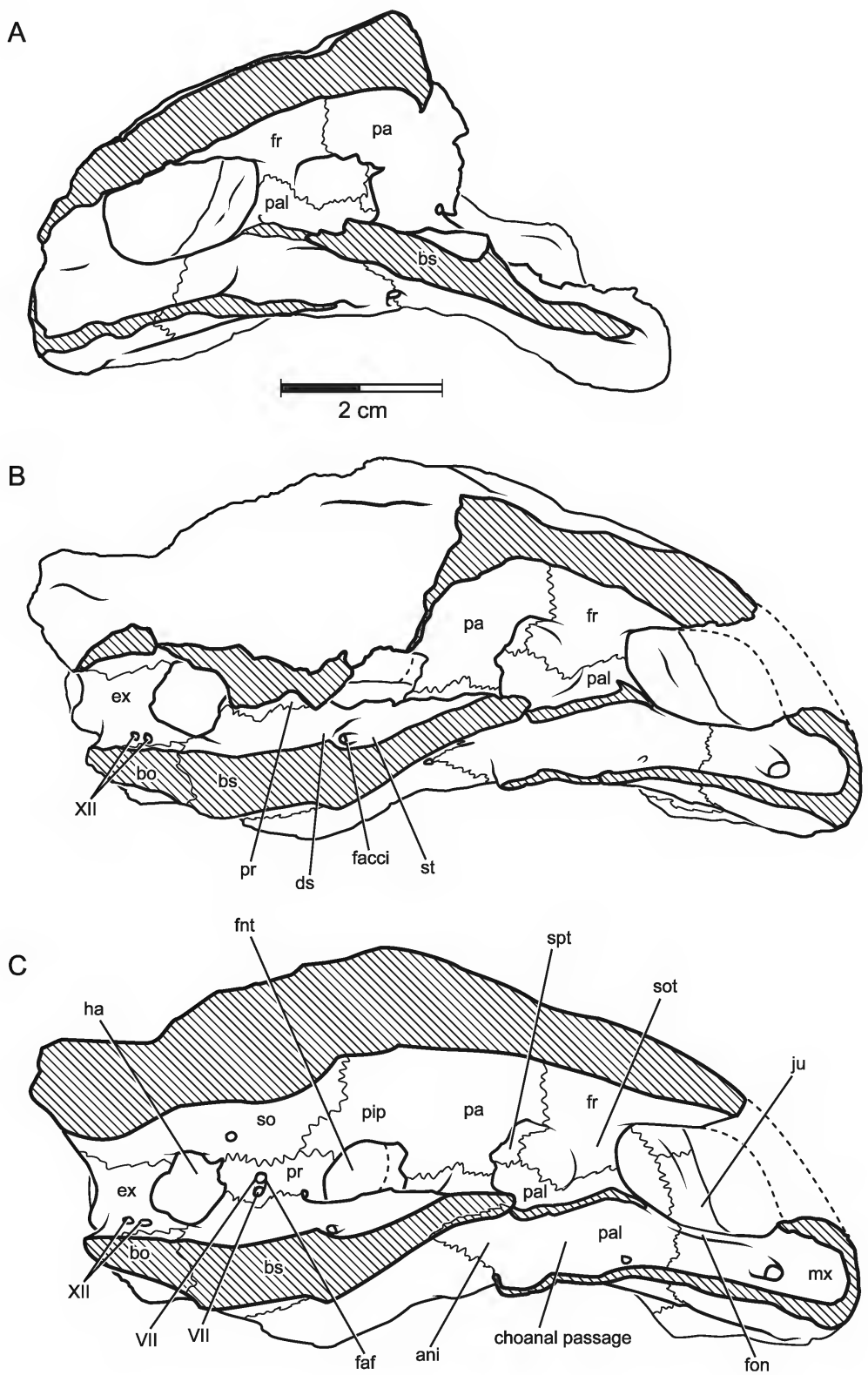



Fig. 65. *Brontochelys gaffneyi* (Wood), n. gen. BMNH R.8570. Skull. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [E.E. Nixon, del.]

forms the posterodorsal rim of the orbit as in the other subtribe Stereogenyina.

**Contacts of medial process:** In the anterior view of the septum orbitotemporale the postorbital contacts the frontal dorsomedially, the palatine ventromedially, and the jugal ventrally. In posterior view of the septum orbitotemporale the postorbital con-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tacts the parietal dorsomedially, the pterygoid ventromedially, and the jugal ventrolaterally.

**Structures of medial process:** The postorbital of *Brontochelys* participates in the formation of the septum orbitotemporale.

PREMAXILLA

The premaxilla is not preserved in BMNH R.8570.

MAXILLA

**Preservation:** Most of both maxillae are preserved in BMNH R.8570, but the anterior sutural contacts with the premaxillae are damaged and lack sutural surfaces, so the anteromedial extent of the maxilla is unknown. However, the close similarity with other subtribe Stereogenyina suggests that little of either maxilla is missing. Similarly, the posterior edge of the maxilla on each side is a broken surface with no indication of a sutural contact.

**Contacts and structures of vertical plate:** As preserved, the maxilla in *Brontochelys* contacts only the prefrontal anterodorsally and the jugal posterodorsally. The maxilla forms the ventral margin of the orbital rim. There is no remnant of the cheek formation. The orbital rim in *Brontochelys* defines an opening that faces more anteriorly than laterally, as in all subtribe Stereogenyina, but in *Brontochelys* the orbit faces even more anteriorly than in *Latentemys*, *Cordichelys*, *Shweboemys*, and *Stereogenys*. It is about the same as in *Bairdemys venezuelensis* and *Lemurchelys*. The maxilla shape reflects the snout shape and *Brontochelys* has an unusually broad snout.

**Contacts of horizontal plate:** The maxilla as preserved in *Brontochelys* contacts the jugal posterolaterally and the palatine posteriorly.

**Structures of horizontal plate:** The maxilla makes up the anterior half of the secondary palate in BMNH R.8570, as in the other subtribe Stereogenyina. It forms the choanal passage that divides the internal nares from the braincase proper. There is a large foramen orbitonasale communicating between the choanal passage and the fossa orbitalis as in the other subtribe Stereogenyina. The median opening that divides the secondary palate has no anterior margin because the premaxillae are missing. The median opening is curved on both sides in *Brontochelys* as in *Latentemys*, but in contrast to *Stereogenys* in which the median opening is parallel.

VOMER

There is no indication that a vomer was present in *Brontochelys*.

PALATINE

**Preservation:** Both palatines are preserved in BMNH R.8570. They lack some of the thin bone on the dorsal roof of the choanal passages and the medial margins have a few breaks, but otherwise they are complete.

**Contacts:** As in the other subtribe Stereogenyina the palatine in *Brontochelys* contacts the maxilla anteriorly, the other palatine medially on midline above the secondary palate, and the pterygoid posteriorly. On the dorsal surface the palatine contacts a robust ventral process from the frontal and the anterior part of the processus inferior parietalis.

**Structures on dorsal surface:** The palatine in *Brontochelys* makes up a major part of the fossa orbitalis floor, as in other subtribe Stereogenyina, and the dorsal process forms the ventromedial edge of the septum orbitotemporale. In the subtribe Stereogenyina the fossa orbitalis has a posterior concavity that is greater than in other podocnemidids. In *Brontochelys* the fossa orbitalis concavity is shallower than in the other subtribe Stereogenyina, even though the fossa itself is relatively larger. The dorsal palatine process in *Brontochelys* does not reach the parietal as in *Shweboemys* and *Stereogenys*.

**Structures on ventral surface:** The palatine forms the posterior half of the secondary palate in *Brontochelys*, and the posterior

←

Fig. 66. *Brontochelys gaffneyi* (Wood), n. gen. BMNH R.8570. Medial views of internal cavum cranii. **A,** anterior moiety of right side; **B,** complete moiety of left side; **C,** restored sagittal view of left side. [J. Sharkey, del.]

margin of the apertura narium interna. The choanal passage that connects the apertura narium externa with the apertura narium interna is formed posteriorly by the palatine. The palatine forms not only the primary palate but the secondary one as well. In *Brontochelys* the medial margin is curved as in *Bairdemys*. There is no large foramen palatinum posterius in the subtribe Stereogenyina as in other pleurodires, but a small foramen in BMNH R.8570 is in the right place and on both sides, and may be this foramen.

QUADRATE

**Preservation:** In BMNH R.8570 the only parts of the quadrate remaining are small medial portions attached to the otic chambers. All of the cavum cranii and lateral portions are missing. On the right side the quadrate below the fenestra postotica remains and on the left side a small part next to the basisphenoid remains.

**Contacts and structures:** The only contacts remaining in *Brontochelys* are with the basisphenoid medially and the basioccipital posteromedially. The quadrate forms part of the medial wall of the cavum ptergoidei on the right side and the floor of the groove leading from the incisura columellae auris to the fenestra ovalis, as in other subtribe Stereogenyina.

PTERYGOID

**Preservation:** Both pterygoids in BMNH R.8570 are preserved, but lack the pterygoid flanges and thin bone around the cavum pterygoidei on both sides. The left cavum is filled with matrix; the right one is open laterally. The lateral edges of the processus trochlearis pterygoidei are abraded as well.

**Contacts on ventral surface:** As in the other subtribe Stereogenyina the pterygoid in *Brontochelys* contacts the palatine anteriorly, the other pterygoid anteromedially, the basisphenoid posteromedially, and the quadrate posterolaterally.

**Structures on ventral surface:** The processus trochlearis pterygoidei in *Brontochelys* lies at approximately a right angle to the midline, as in other subtribe Stereogenyina. The cavum pterygoidei is filled with matrix on the left side but broken open on the right. It is formed as in other subtribe Stereogenyina by the pterygoid ventrally, the quadrate posterolaterally, the basisphenoid medially, and the prootic anterolaterally. It is relatively large as in other subtribe Stereogenyina, such as *Bairdemys* and *Latentemys*. The anterior wall of the cavum pterygoidei is open also as in other subtribe Stereogenyina as well as *Erymnochelys* and *Peltocephalus*. On the right side of BMNH R.8570 the foramen cavernosum can be seen in the roof of the cavum cavernosum, indicating the absence of the anterior wall of the cavum. The very short canalis cavernosum and the nearby entry into it can also be seen here. Although the pterygoid flange is not preserved, its base is present on both sides of BMNH R.8570 and it has the full extent seen in other podocnemidids.

**Contacts on dorsal surface:** In the posterior wall of the septum orbitotemporale in *Brontochelys* the pterygoid contacts the palatine ventrally, the jugal anterolaterally, the postorbital dorsolaterally, and the parietal anterodorsally. The parietal contact is relatively wide in comparison to the contact in *Podocnemis*. In the crista pterygoidea the pterygoid contacts the parietal anterodorsally, the prootic posterodorsally. Anteriorly on the dorsal surface the pterygoid contacts the palatine anteriorly and the basisphenoid medially.

**Structures on dorsal surface:** The foramen nervi trigemini in *Brontochelys* has its anterior edge damaged, but it was formed by the pterygoid ventrally, the parietal anterodorsally, and the prootic posterodorsally. The sulcus palatinopterygoideus in *Brontochelys* and the other subtribe Stereogenyina is a large tunnel with thick bone laterally. Its floor is formed by the pterygoid posteriorly and the palatine anteriorly.

SUPRAOCCIPITAL

**Preservation:** The ventral portion of the supraoccipital is complete in BMNH R.8570, but the dorsal portion, the crista supraoccipitalis, is broken away for its entire length.

**Contacts:** As in the other podocnemidids the supraoccipital in *Brontochelys* contacts the parietal anterodorsally, the prootic anterolaterally, the opisthotic posterolaterally, and the exoccipital posteroventrally.

**Structures:** The crista supraoccipitalis extended at least to the foramen magnum.

EXOCCIPITAL

**Preservation:** Both exoccipitals are preserved in BMNH R.8570. They are both somewhat eroded along their posterolateral edges, but otherwise seem complete. The sutures in some areas are indistinct.

**Contacts:** The exoccipital of *Brontochelys* has the usual contacts with the supraoccipital dorsally, the opisthotic laterally, the quadrate ventrolaterally, and the basioccipital ventrally.

**Structures:** The condylus occipitalis is broken distally in BMNH R.8570, but the two exoccipitals and the basioccipital can be seen in the preserved base. The foramina nervi hypoglossi leave the skull in two foramina, but the exit is united as one recessed foramen, as in nearly all other subtribe Stereogenyina. The foramen jugulare posterius is closed completely by the exoccipital.

BASIOCCIPITAL

**Preservation:** The basioccipital in BMNH R.8570 has some erosion along its lateral margins and some of the contacts are unclear.

**Contacts:** As in other subtribe Stereogenyina the basioccipital in BMNH R.8570 contacts the basisphenoid anteriorly, the quadrate laterally, the exoccipital posterodorsally, and the opisthotic dorsolaterally.

**Structures:** The basioccipital in *Brontochelys* is relatively short, shorter than in *Bairdemys venezuelensis*, but not as short as in its near relatives, *Stereogenys* and *Shweboemys*.

PROOTIC

**Preservation:** Both prootics are preserved in BMNH R.8570, the right one is complete and the left one has some damage around the lateral contact with the pterygoid in the wall of the cavum pterygoidei.

**Contacts:** As in the other subtribe Stereogenyina, the prootic contacts in BMNH R.8570 are with the parietal anterodorsally, the quadrate laterally, the supraoccipital dorsally, the basisphenoid ventromedially (on the medial side of the cavum pterygoidei), the pterygoid ventrolaterally (on the lateral side of the cavum pterygoidei), and the opisthotic posteriorly.

**Structures:** The foramen nervi trigemini in *Brontochelys* is formed by the prootic posterodorsally, the parietal anterodorsally, and the pterygoid ventrally, as in other podocnemidids. The foramen stapedio-temporale is formed by the prootic medially and the quadrate laterally, as in most turtles. As in other subtribe Stereogenyina as well as in *Mogharemys* and *Erymnochelys*, the foramen cavernosum lies in the roof of the cavum pterygoidei formed by the quadrate and prootic. The prootic forms the anterior margin of the hiatus acusticus, visible in BMNH R.8570. Just anterior to it the fossa acustico-facialis contains the more ventral foramen nervi facialis (VII) and the more dorsal foramen nervi acustici (VIII).

OPISTHOTIC

**Preservation:** Both opisthotics are present in BMNH R.8570 and both lack their distal ends.

**Contacts:** As in other podocnemidids the opisthotic of *Brontochelys* contacts the supraoccipital anteromedially, the prootic anteriorly, the quadrate laterally, and the exoccipital posteromedially. The squamosal is not preserved, so that possible contact is indeterminate.

**Structures:** The opisthotic in *Brontochelys* forms the roof and medial wall for the fenestra postotica. The lateral wall of the fenestra postotica is not preserved.

BASISPHENOID

**Preservation:** The basisphenoid in BMNH R.8570 is nearly complete.

**Contacts on ventral surface:** The basisphenoid in *Brontochelys* contacts the pterygoid anterolaterally, the basioccipital posteriorly, and the quadrate laterally.

**Structures on ventral surface:** The basisphenoid forms the medial wall and part of the floor and roof of the cavum pterygoidei. *Brontochelys* has the anteriorly open condition of the cavum, and the basisphenoid has the foramen posterius canalis carotici interni in its lateral surface. This surface is somewhat concave as well, due to the large size of the cavum pterygoidei.

The basisphenoid in *Brontochelys* is wider than the basioccipital in contrast to all other subtribe Stereogenyina in which it is the same or narrower.

**Contacts on dorsal surface:** The basisphenoid of *Brontochelys* contacts the pterygoid anterolaterally, the prootic laterally, the palatine anteriorly, and the basioccipital posteriorly, as in other podocnemidids.

**Structures on dorsal surface:** *Brontochelys* has a low, not overhanging, dorsum sellae, a shallow sella turcica, and a long but low rostrum basisphenoidale, in contrast to the higher dorsum sellae, deeper sella turcica, and more sharply defined rostrum basisphenoidale of *Latentemys*. The sulcus cavernosus in *Brontochelys* is a relatively wide groove confluent with the cavum pterygoidei, as in the rest of the taxa with an anteriorly open cavum. The foramen anterius canalis carotici interni is in the lateral edge of the shallow sella turcica and opens directly anteriorly from the short canalis caroticus internus. There is no apparent processus clinoideus.

*Lemurchelys*
Figures 67–70

This taxon is based on the sole skull, DPC 6425. The skull is generally well preserved but has a thin coating of iron oxide covering some parts. The occiput and left septum orbitotemporale have been abraded and lost some of their original surface. Most of the left otic chamber is missing and the skull roofing elements are also gone.

PREFRONTAL

**Preservation:** Both prefrontals are preserved and complete in DPC 6425. The anterior margins of both bones are preserved; frequently broken in the subtribe Stereogenyina.

**Contacts:** The prefrontal in Duke contacts the prefrontal on the midline, the maxilla anteroventrolaterally, and the frontal posteriorly, as in the other subtribe Stereogenyina.

**Structures:** The dorsal margin of the apertura narium externa is slightly protruding, but not to the extent seen in *Bairdemys venezuelensis*.

FRONTAL

**Preservation:** Both frontals are present and complete.

**Contacts:** The frontal in DPC 6425 contacts the other frontal on the midline, the prefrontal anteriorly, the postorbital posterolaterally, the parietal posteriorly, and the palatine ventrally, as in all other subtribe Stereogenyina.

**Structures:** The frontal in DPC 6425 forms a relatively small section of the dorsal orbital rim, less than in other subtribe Stereogenyina and much less than in *Cordichelys* and *Brontochelys*.

PARIETAL

**Preservation:** The parietals in DPC 6425 are present only anteromedially, the posterior and lateral portions forming the fossa temporalis covering are broken away.

**Contacts and structures of dorsal plate:** The parietal in DPC 6425 contacts the other parietal on the midline, the frontal anteriorly, and the postorbital laterally. Other cheek contacts are not preserved. The degree of emargination is unknown.

**Contacts and structures of processus inferior parietalis:** The area of contact of the processus inferior parietalis and the crista pterygoidea is largely covered by matrix. The pterygoid-parietal contact can be seen in places. As in other podocnemidids, the parietal contacts the prootic posteroventrally and the supraoccipital posteriorly. The foramen nervi trigemini is formed by the parietal anterodorsally, the prootic dorsolaterally, and the pterygoid ventrally. The parietal forms part of the roof of the sulcus palatinopterygoideus.

JUGAL

**Preservation:** Both jugals are present, but the thin cheek plate covering the fossa temporalis is broken away on both sides, so the presence and extent of the cheek emargination is unknown.

**Contacts of lateral plate:** The preserved portion of the jugal contacts the maxilla anteroventrally and the postorbital dorsally, but the posterior contacts are unknown.

**Structures of lateral plate:** The jugal in Duke 6425 forms most of the posterior orbital rim, as in *Shweboemys* and *Bairdemys* but in contrast to the small portion in *Cordichelys*. The possibility of a cheek emargination is unknown.

**Contacts and structures of medial process:** In the floor of the fossa orbitalis, the jugal contacts the maxilla anteriorly and laterally and the palatine medially, as in *Latentemys*. In the septum orbitotemporale in posterior view, the jugal contacts the postorbital

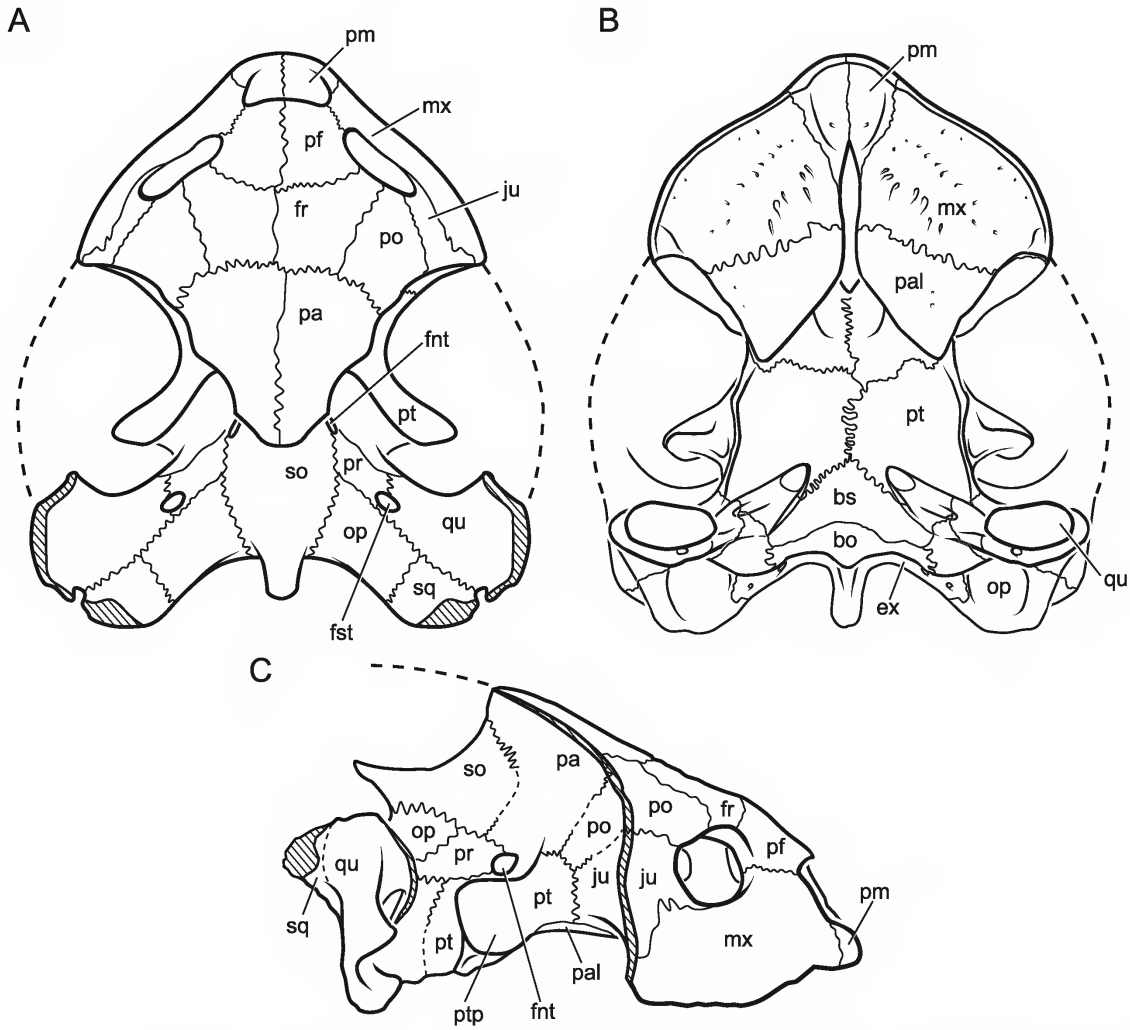


Fig. 67. *Lemurchelys diasphax,* n. gen. et sp. Partially restored skull based on DPC 6425. **A,** dorsal; **B,** ventral; **C,** lateral. [I. Kayama, F. Ippolito, del.]

dorsomedially, the palatine ventromedially, the pterygoid posteriorly and the maxilla ventrally, also as in *Latememys*. There is no contribution to the triturating surface.

QUADRATOJUGAL

The quadratojugal is not preserved in DPC 6425.

SQUAMOSAL

**Preservation:** Very little of the right squamosal and none of the left are preserved. There are some parts of the quadrate-squamosal suture remaining on the right side, including fragments of the squamosal internal bone.

**Contacts and structures:** The quadrate anteriorly and some of the opisthotic suture posteromedially remain and are as in *Latentemys*. The squamosal portion forming the small antrum postoticum is present and can be seen from the anterior opening of the antrum. The external shape of the squamosal is not preserved.

POSTORBITAL

**Preservation:** The anterior and medial portions of both postorbitals are mostly preserved. On the left side a large hole in the middle of the septum orbitotemporale has removed most of the ventral

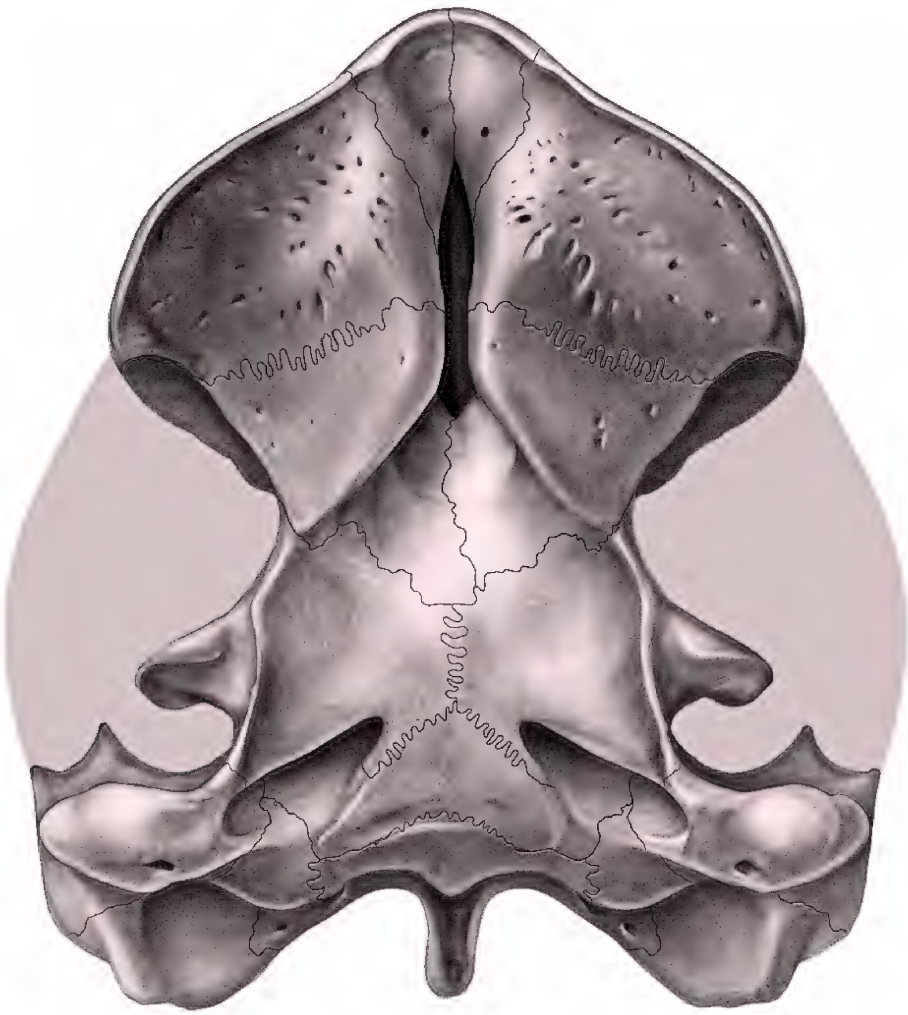

Fig. 68. *Lemurchelys diasphax,* n. gen. et sp. Partially restored ventral view based on DPC 6425. [I. Kayama, del.]

plate, but the dorsal and ventral sutures remain. The thin, posterior sheets covering the fossa temporalis are gone on both postorbitals.

**Contacts of lateral plate:** The preserved contacts of the postorbital are with the frontal anteromedially, the jugal ventrally, and the parietal posteromedially.

**Structures of lateral plate:** The postorbital makes up the posterodorsal part of the orbital rim. The degree of exposure in DPC 6425 is more than in *Shweboemys* and about the same as in *Latentemys* and *Stereogenys.*

**Contacts and structures of medial process:** The anterior surface of the septum orbitotemporale is obscured by a layer of matrix in the fossa orbitalis on both sides of DPV 6425 and the sutures are not clear. In the posterior surface of the septum orbitotemporale, facing the fossa temporalis, the postorbital contacts the parietal dorsomedially, the pterygoid ventromedially, and the jugal ventrolaterally, as in *Latentemys* and *Brontochelys* and in contrast to *Shweboemys* and *Stereogenys* in which the dorsal process of the palatine reaches the postorbital. As in the other subtribe Stereogenyina, the postorbital makes up part of the roof and lateral wall of the sulcus palatinopterygoideus and the dorsal portion of the septum orbitotempor-

ale. The fossa orbitalis in DPC 6425 and the other subtribe Stereogenyina has a posterior enlargement, extending well past the orbital rim, and forming a relatively large cavity behind the eye itself.

PREMAXILLA

**Preservation:** Most subtribe Stereogenyina manage to loose their premaxillae for some reason, but DPC 6425 has both of them complete.

**Contacts:** The premaxilla contacts the maxilla posterolaterally and the other premaxilla medially on the midline.

**Structures on dorsal surface:** The premaxilla forms the floor of the fossa nasalis, with DPC 6425 showing the beginning of the choanal division with a posteriorly rising ridge on the midline. The margin of the apertura narium externa is very blunt and there is no sharp division of the fossa nasalis and the external surface of the skull. A foramen praepalatinum can be seen in each premaxilla extending from the dorsal surface to the ventral surface.

**Structures on ventral surface:** The shape of the premaxilla in DPC 6425 is difficult to compare with that in other subtribe Stereogenyina because most lack the premaxilla. However, DPC 6425 has a slight pinching or protrusion of the anterior snout that is absent in *Latentemys*, *Cordichelys*, and *Bairdemys venezuelensis*, indeterminate (although probably absent) in *Brontochelys*, and present in *Stereogenys* and *Shweboemys*. There is a slight midline concavity not defined posteriorly but sloping dorsally into the apertura narium interna, similar to that seen in *Bairdemys venezuelensis*. There are no accessory ridges. The foramen praepalatinum lies closer to the posterior edge of the premaxilla than to the anterior edge.

MAXILLA

**Preservation:** Both maxillae are present and nearly complete. The labial ridges are slightly damaged and the posteroventral margin is broken.

**Contacts of vertical plate:** The maxilla as preserved contacts the premaxilla anteromedially, the jugal posterodorsally, and the prefrontal anterodorsally.

**Structures of vertical plate:** The ventral margin of the orbital rim is formed by the maxilla and is a rounded, sloping surface, as in *Brontochelys*, not a sharp ridge as in all other subtribe Stereogenyina. The apertura narium externa in DPC 6425 is similar in shape to that in *Bairdemys venezuelensis*. The apertura is damaged or missing in other subtribe Stereogenyina precluding useful comparisons. There is no remnant of possible cheek emargination.

**Contacts of horizontal plate:** The horizontal plate of the maxilla in DPC 6425 contacts the premaxilla anteromedially, the palatine posteromedially, and the jugal posterolaterally.

**Structures of horizontal plate:** The triturating surface in DPC 6425 is similar to that in *Stereogenys* and *Shweboemys* and different from all other subtribe Stereogenyina, in having parallel medial margins forming the apertura narium interna. However, the length of the secondary palate is shorter in DPC 6425 than in the other two genera. There is a slight convexity on the maxilla in DPC 6425, similar to that in *Cordichelys* and much smaller than in *Bairdemys venezuelensis*. The labial ridge is blunt and rounded in DPC 6425, similar to that in *Shweboemys* but different from the higher, but still blunt, ridge in *Stereogenys*. The maxilla in DPC 6425 is relatively thick and swollen as in *Shweboemys*, in contrast to the thin and narrow maxilla of *Latentemys* and *Cordichelys*.

VOMER

It can be determined that there is no vomer in DPC 6425.

PALATINE

**Preservation:** Both palatines are present and complete in DPC 6425.

**Contacts:** The palatine contacts the maxilla anterolaterally and the pterygoid posteriorly. On the dorsal surface the palatine contacts the processus inferior parietalis. The sutures in the fossa orbitalis are difficult to make out due to matrix, but there is the usual palatine-maxilla anteriorly and the palatine-jugal anterolaterally.

**Structures on dorsal surface:** DPC 6425 shows the choanal passages extending from the apertura narium externa posteriorly into the cleft-shaped apertura narium interna. The palatine forms the posterior part of this secondary palate and the maxilla forms the

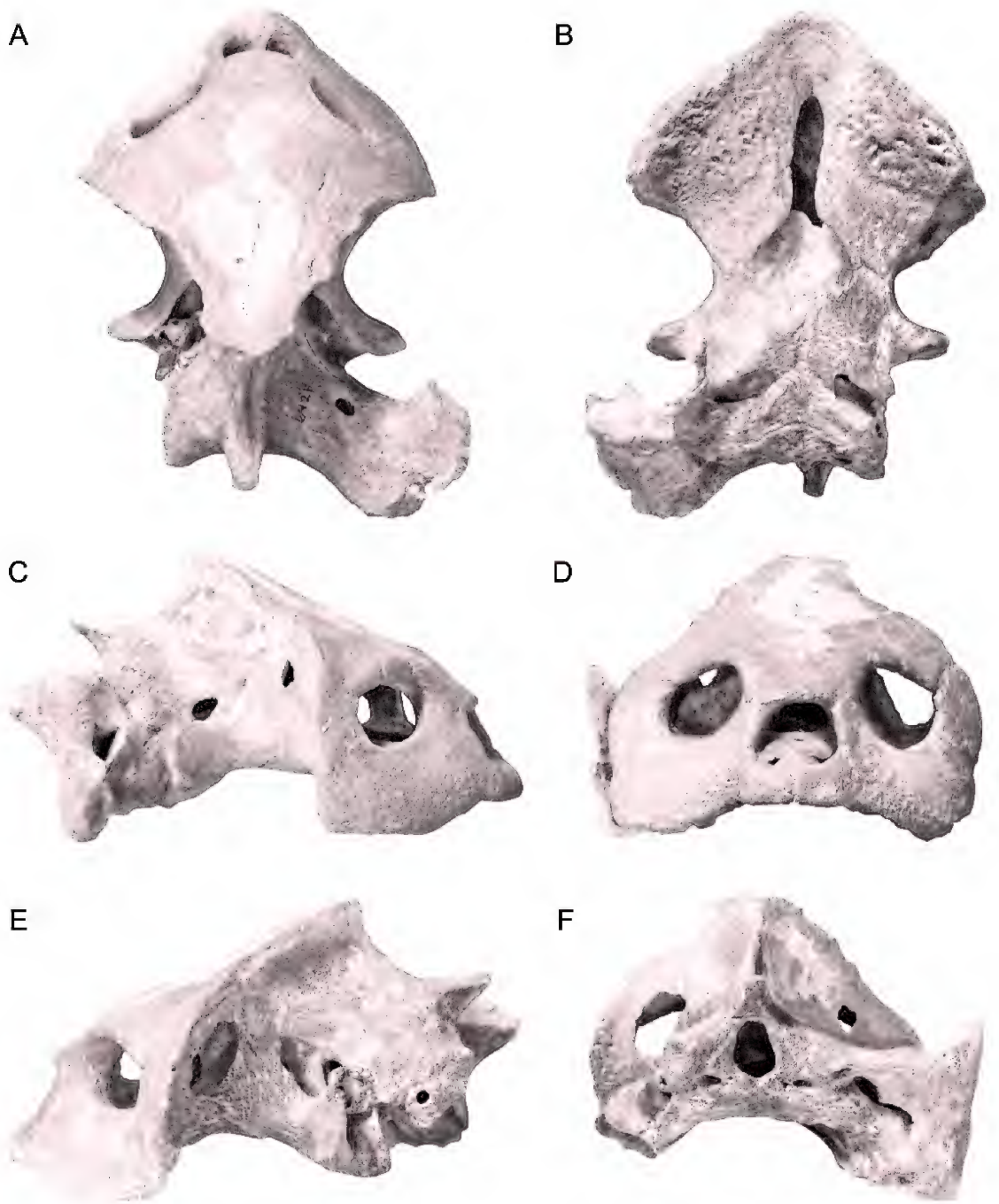


Fig. 69. *Lemurchelys diasphax,* n. gen. et sp. DPC 6425. Skull. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [E.E. Nixon, del.]

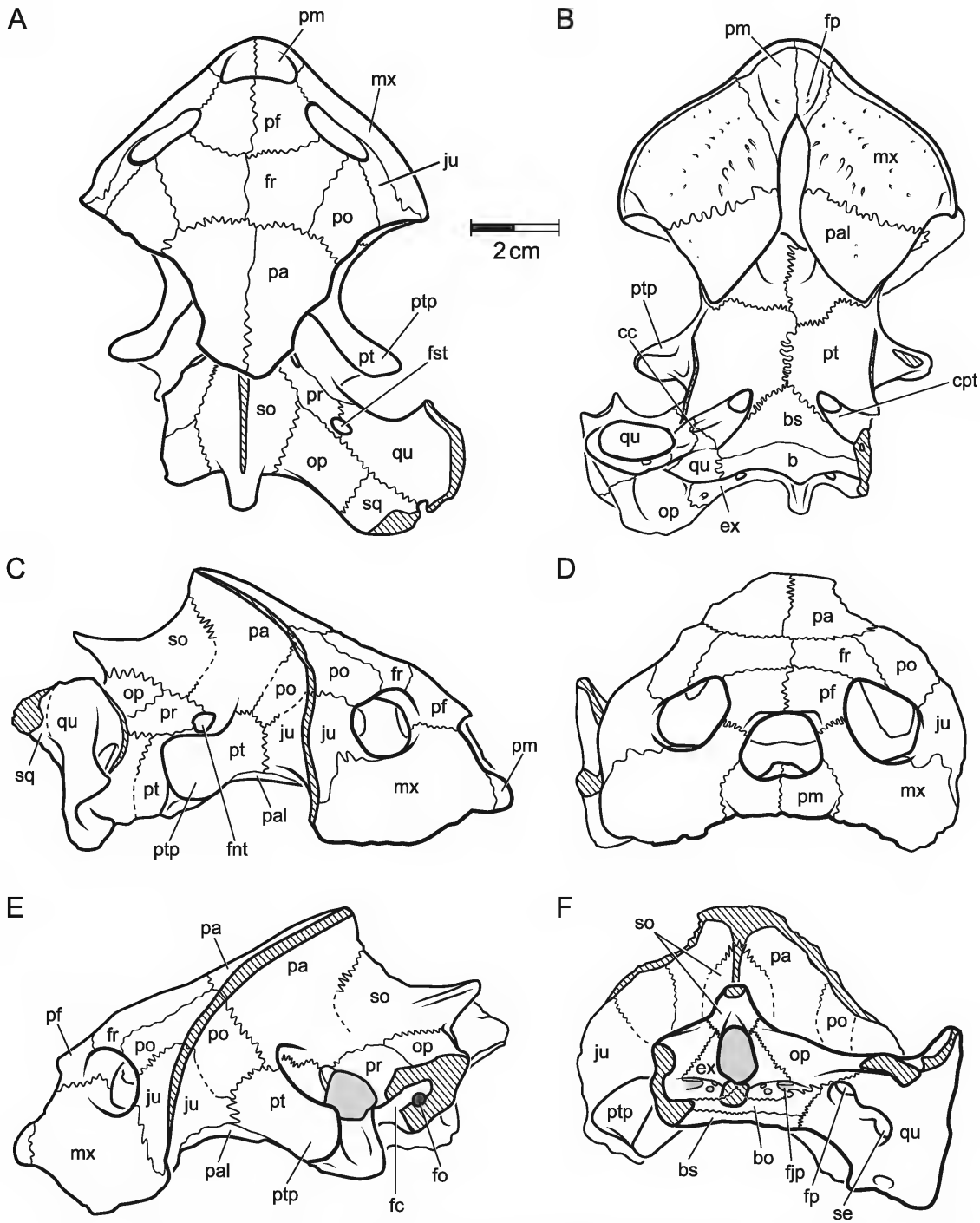


Fig. 70. *Lemurchelys diasphax,* n. gen. et sp. DPC 6425. Skull. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [F. Ippolito, del.]

anterior part. There is no indication of a foramen palatinum posterius in DPC 6425.

**Structures on ventral surface:** The palatine is slightly shorter than the maxilla in DPC 6425, in contrast to *Shweboemys* and *Stereogenys*, which have palatines that are longer than the maxilla. The palatine surface is slightly concave, as in *Latentemys* and *Cordichelys*, not as deep as in *Bairdemys venezuelensis*.

QUADRATE

**Preservation:** Only the posterior part of the right quadrate is present in DPC 6425. None of the cheek or skull roof contacts remain.

**Contacts on lateral surface:** The only remaining contact on the quadrate lateral surface is with the squamosal posterodorsally.

**Structures on lateral surface:** The posterior part of the cavum tympani is preserved, showing the enclosed incisura columellae auris containing the eustachian tube and stapes. The eustachian tube is not separated by bone from the fenestra postotica in DPC 6425. The antrum postoticum is very small and tubular, as in *Stereogenys*, not flat as in *Bairdemys venezuelensis*. The fossa precolumellaris is not preserved.

**Contacts on dorsal and anterior surface:** The quadrate contacts the prootic anteromedially, the opisthotic posteromedially, and the squamosal posteriorly and posterolaterally.

**Structures on dorsal and anterior surface:** Although the surfaces of both otic chambers are slightly abraded, the foramen stapediotemporale is clearly preserved on the right side. It is oriented anterodorsally, as in the other subtribe Stereogenyina in which it is preserved.

**Contacts on ventral surface:** The quadrate contacts the pterygoid anteromedially, the basisphenoid medially, the basioccipital posteromedially, and the prootic medially, as in the other subtribe Stereogenyina.

**Structures on ventral surface:** The cavum pterygoidei is formed laterally and dorsally by the quadrate in podocnemidids, and this is the case in DPC 6425. The lateral extent of the cavum, however, is deeper in DPC 6425 than in other subtribe Stereogenyina, being similar in extent to that in *Mogharemys*. In the roof of the cavum pterygoidei is the opening of the canalis cavernosus, the foramen cavernosum, formed mostly by the prootic but with some quadrate entering into its margin. Just ventromedial to the foramen cavernosum, is a much smaller foramen, the foramen nervi facialis. The full cavum pterygoidei is preserved on the right side of DPC 6425. On the left side the cavum is broken about midway along its length, showing a section of the foramen cavernosum.

**Contacts on posterior surface:** The posterior surface of DPC 6425 is abraded to a varying extent and some of the visible sutures are actually below the original bone level. The quadrate in DPC 6425 contacts the squamosal dorsolaterally, the opisthotic dorsomedially, and the basioccipital ventromedially.

**Structures on posterior surface:** The fenestra postotica in DPC 6425 is not separated by bone from the sulcus eustachii as in *Bairdemys* and *Latentemys*, but is confluent as in *Stereogenys*. The incisura columellae auris is visible posteriorly and is intact on the right side of DPC 6425; on the left side it is broken revealing its medial shape as an oval tunnel. The presence of the foramen chorda tympani inferius cannot be determined due to abrasion and matrix in DPC 6425.

PTERYGOID

**Preservation:** The pterygoid is present on both sides of DPC 6425, but they are damaged posteriorly with the floor of the cavum pterygoidei eroded away exposing the interior. The pterygoid flanges are broken away on both sides.

**Contacts on ventral surface:** The pterygoid in DPC 6425 contacts the palatine anteriorly, the other pterygoid medially, the basisphenoid posteromedially, and the quadrate posterolaterally, as in the other subtribe Stereogenyina.

**Structures on ventral surface:** The processus trochlearis pterygoidei in DPC 6425 is similar to that in the other subtribe Stereogenyina, it lies at right angles to the midline and has a small concavity at its base on the ventral surface. The cavum pterygoidei is floored by the pterygoid, although in DPC 6425 the floor is mostly eroded away. The presence of a pterygoid flange is revealed by the presence of its base, but its extent is not

determinable. There is no sign of a foramen palatinum posterius, and the palatine-pterygoid suture area is well preserved on the left side of DPC 6425, so if one were present it would probably be visible. See Quadrate for cavum pterygoidei description.

**Contacts on dorsal surface:** The contacts of the pterygoid at the base of the processus trochlearis pterygoidei are with the postorbital dorsolaterally, the jugal anterolaterally, the palatine anteroventrally, and the parietal anterolaterally. The contacts of the crista pterygoidea are unclear due to matrix, but these contacts are visible: the parietal anterodorsally, the prootic posterodorsally, the quadrate posterolaterally, and the palatine anteriorly.

**Structures on dorsal surface:** The sulcus palatinopterygoideus and its associate septum orbitotemporale are formed in DPC 6425 as in *Latentemys*, by the postorbital, parietal, pterygoid, and palatine. Also as in the other subtribe Stereogenyina, the foramen nervi trigemini in DPC 6425 is formed by the parietal anterodorsally, the prootic dorsolaterally, and the pterygoid ventrally.

SUPRAOCCIPITAL

**Preservation:** Only the base of the supraoccipital is preserved in DPC 6425, the crista supraoccipitalis is broken away.

**Contacts:** As in other subtribe Stereogenyina the supraoccipital in DPC 6425 contacts the parietals dorsally and anteriorly, the prootic anterolaterally, the opisthotic posterolaterally, and the exoccipitals posteroventrally.

**Structures:** Although most of the structure is broken away, the base of the crista in DPC 6425 is much deeper than in *Cordichelys, Stereogenys*, and *Shweboemys*.

EXOCCIPITAL

**Preservation:** Both exoccipitals are present in DPC 6425, but they are abraded on their posterior surface, showing some of the sutures below the original bone surface.

**Contacts:** The exoccipital in DPC 6425 contacts the supraoccipital dorsally, the opisthotic laterally, and the basioccipital ventrally.

**Structures:** Although broken off, the base of the condylus occipitalis shows the typical tripartite structure of two exoccipitals and a median basioccipital. In contrast to all other subtribe Stereogenyina except *Bairdemys sanchezi*, the foramen nervi hypoglossi are two separate openings not combined into a single recessed opening. It is possible that this is the result of the abrasion and erosion of the occipital surface seen in DPC 6425, but it is the same on both sides and this seems unlikely. The foramen jugulare posterius is closed by bone, which seems to include the opisthotic and basioccipital, although this may be due to damage.

BASIOCCIPITAL

**Preservation:** The basioccipital in DPC 6425 is mostly present, but its surface is damaged by abrasion. The left lateral edge is broken.

**Contacts:** The basioccipital contacts the basisphenoid anteriorly, the quadrate laterally, the exoccipitals posterodorsally, and the opisthotic laterally.

**Structures:** Compared with forms like *Latentemys* and *Cordichelys*, DPC 6425 has no distinct tuberculum basioccipitale. However, this area is abraded and it is likely that these were worn away. The basioccipitale of DPC 6425 is sufficiently worn to look more like the very short basioccipitale in *Stereogenys* and *Shweboemys*. However, this does not seem to be the case when compared with surrounding elements to get a better idea of its length.

PROOTIC

**Preservation:** The right prootic in DPC 6425 is complete, the left one lacks some of its lateral edges due to the breakage of the otic chamber at this position.

**Contacts:** The prootic contacts the parietal dorsomedially, the quadrate laterally, the supraoccipital posterodorsally, the pterygoid ventrally, the basisphenoid ventrally, and the opisthotic posteriorly, as in other podocnemidids.

**Structures:** The prootic in DPC 6425 is very similar to that bone in the other subtribe Stereogenyina. It has a smooth surface medial to the foramen stapedio-temporale, rather than the raised convexity seen in *Cordichelys* and *Latentemys*. The prootic forms part of the foramen cavernosum in the roof of the cavum pterygoidei, and this can be seen in section on the left side of DPC 6425.

OPISTHOTIC

**Preservation:** The right opisthotic is preserved in DPC 6425, but it is incomplete laterally and its sutures are unclear in some places due to an iron oxide crust.

**Contacts:** Enough of the contacts can be made out to see that they are as in other podocnemidids: the supraoccipital anteromedially, the prootic anteriorly, the quadrate anterolaterally, the squamosal posterolaterally, and the exoccipital posteromedially.

**Structures:** The opisthotic forms the lateral wall of the foramen jugulare posterius and the medial wall of the fenestra postotica.

BASISPHENOID

**Preservation:** The basisphenoid in DPC 6425 is nearly complete. It lacks a small portion of its lateral margin and its contacts with the pterygoids are eroded away along with the flooring of the cavum pterygoidei. Only the ventral surface is visible.

**Contacts on ventral surface:** The basisphenoid contacts the pterygoids anterolaterally, the basioccipital posteriorly, the prootic dorsolaterally (within the cavum pterygoidei), and the quadrate laterally.

**Structures on ventral surface:** The basisphenoid shape differs from that in *Stereogenys* and *Shweboemys* in being much wider than long as in *Brontochelys*. The basisphenoid makes up the medial wall of the cavum pterygoidei, although the sutures here are unclear.

## *Shweboemys*
Figures 71–74

This taxon is based on two skulls, GSI 17255 (holotype) and BMNH R.8432. Both skulls are similar in state of preservation: they both lack the otic chambers, most of the occiput, and skull roofing elements covering the fossa temporalis. As we have been able to see only BMNH R.8432, nearly all of the following is based on it. Observations on GSI 17255 are based on the literature (Swinton, 1939: figs. 1, 2; Wood, 1970: pl. 1, figs. A, B). The internal part of the skull in BMNH R.8432 is filled with matrix and unavailable at present for examination. Of the two skulls, BMNH R.8432 is the more complete.

PREFRONTAL

**Preservation:** Both prefrontals are preserved and nearly complete in GSI 17255, and BMNH R.8432. The anterior margins in both specimens are broken, although BMNH R.8432, is more complete. The dorsal margin of the apertura narium externa in BMNH R.8432 appears to have only a small amount of bone missing or perhaps nothing is missing at all.

**Contacts:** The prefrontal in *Shweboemys* contacts the other prefrontal on the midline, the maxilla anteroventrolaterally, and the frontal posteriorly, as in the other subtribe Stereogenyina.

**Structures:** As preserved, the dorsal margin of the apertura narium externa in BMNH R.8432 has no anterior protrusion seen in some other subtribe Stereogenyina, e.g., *Bairdemys*. It is very similar in extent to that seen in *Lemurchelys*.

FRONTAL

**Preservation:** Both frontals are present and complete in GSI 17255 and BMNH R.8432. The ventral surfaces are covered by matrix in the latter.

**Contacts:** The frontal in *Shweboemys* contacts the other frontal on the midline, the prefrontal anteriorly, the postorbital posterolaterally, the parietal posteriorly, and the palatine ventrally, as in all other subtribe Stereogenyina.

**Structures:** The frontal forms a section of the dorsal orbital rim, with less exposure than in *Brontochelys* but more than in *Lemurchelys*.

PARIETAL

**Preservation:** The parietals in GSI 17255 and BMNH R.8432 are present only anteromedially; the posterior and lateral portions forming the fossa temporalis covering are broken away.

**Contacts and structures of dorsal plate:** The parietal in *Shweboemys* contacts the other parietal on the midline, the frontal anteriorly, and the postorbital laterally. Other cheek contacts are not preserved. The degree of emargination is unknown. In the septum orbitotemporale the parietal contacts the postorbital anteriorly, the palatine anteroventrally, and the pterygoid ventrally (fig. 74F).

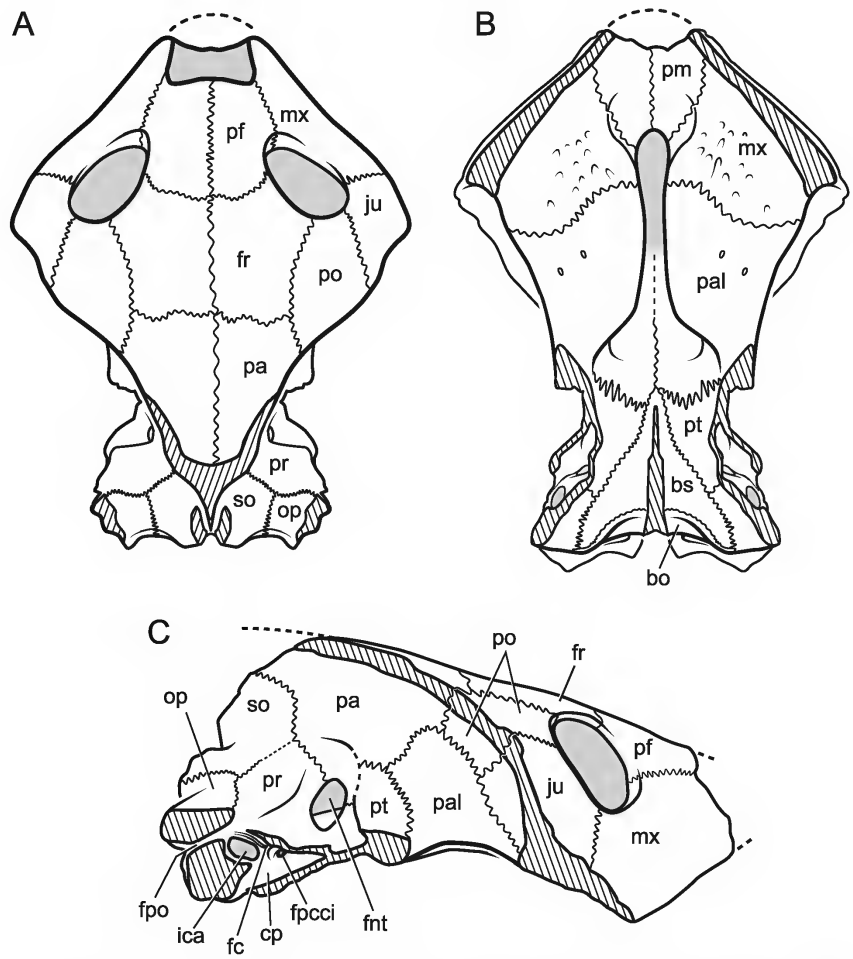


Fig. 71. *Shweboemys pilgrimi* Swinton, 1939. Partially restored skull based on BMNH R.8432. **A,** dorsal; **B,** ventral; **C,** lateral. [F. Ippolito, del.]

**Contacts and structures of processus inferior parietalis:** Only the most posterior part of the processus inferior parietalis is visible in BMNH R.8432. It contacts the pterygoid ventrally and forms the anterodorsal rim of the foramen nervi trigemini.

JUGAL

**Preservation:** Both jugals are present in BMNH R.8432, but the thin cheek plate covering the fossa temporalis is broken away on both sides, so the presence and extent of the cheek emargination is unknown. The left jugal has visible sutures, but the right one is covered by matrix. The presence and extent of the jugal in GSI 17255 is not known to us.

**Contacts of lateral plate:** The preserved portion of the jugal in BMNH R.8432 contacts the maxilla anteroventrally and the postorbital dorsally, but the posterior contacts of the lateral plate are unknown.

**Structures of lateral plate:** The jugal in *Shweboemys* forms most of the posterior orbital rim, as in *Bairdemys* but in contrast to the small portion in *Cordichelys*. The possibility of a cheek emargination is unknown.

**Contacts and structures of medial process:** In the septum orbitotemporale in posterior view in BMNH R.8432, the jugal contacts the postorbital dorsomedially, the palatine posteromedially, and the maxilla

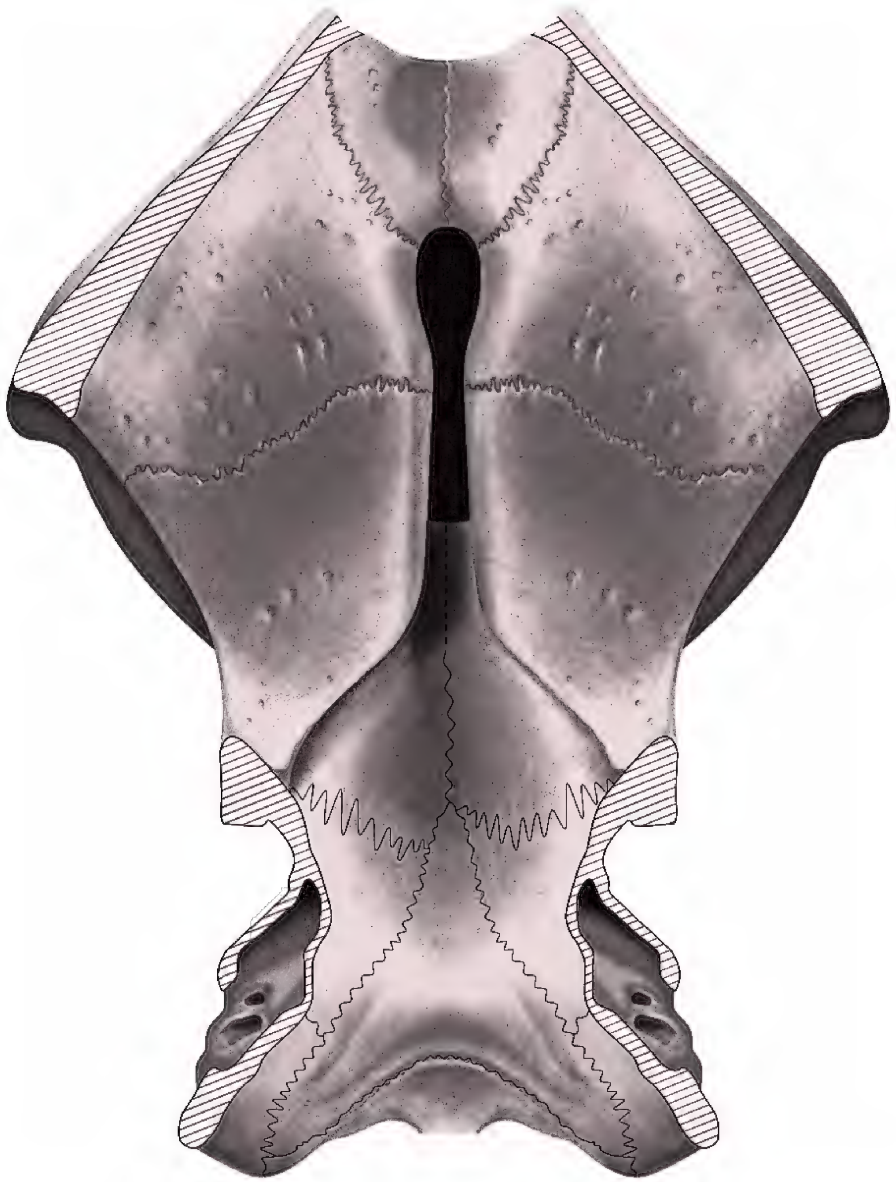

Fig. 72. *Shweboemys pilgrimi* Swinton, 1939. Partially restored ventral view based on BMNH R.8432. [M. Rightmyer, del.]

ventrally, as in *Stereogenys*, but in contrast to all other subtribe Stereogenyina. The wide dorsal process of the palatine prevents a jugal-pterygoid contact. There is no jugal contribution to the triturating surface.

QUADRATOJUGAL

The quadratojugal is not preserved in GSI 17255 and BMNH R.8432.

SQUAMOSAL

The squamosal is not preserved in GSI 17255 and BMNH R.8432.

POSTORBITAL

**Preservation:** The anterior and medial portions of both postorbitals are mostly preserved in BMNH R.8432. The thin, posterior sheets covering the fossa temporalis are gone on both postorbitals.

**Contacts of lateral plate:** The preserved contacts of the postorbital are with the frontal anteromedially, the jugal ventrally, and the parietal posteromedially.

**Structures of lateral plate:** The postorbital makes up the posterodorsal part of the orbital rim. The degree of exposure in *Shweboemys* is about the same as in *Latentemys* and *Stereogenys*.

**Contacts and structures of medial process:** In the posterior surface of the septum orbitotemporale, facing the fossa temporalis, the postorbital contacts the parietal dorsomedially, the palatine ventromedially, and the jugal ventrally. As in the other subtribe Stereogenyina, the postorbital makes up part of the roof and lateral wall of the sulcus palatinopterygoideus and the dorsal portion of the septum orbitotemporale. The presence of a fossa orbitalis posterior enlargement is not determinable.

PREMAXILLA

**Preservation:** The premaxilla is present in BMNH R.8432, but both are broken anteriorly. In GSI 17255 the Swinton figure (1939: fig. 2) shows no premaxillae, but the photo in Wood (1970: pl. 1) has what could be interpreted as premaxillae. In any case, the latter specimen is less complete than BMNH R.8432.

**Contacts:** The premaxilla contacts the maxilla posterolaterally and the other premaxilla medially on the midline.

**Structures on dorsal surface:** The ventral margin of the apertura narium externa is not preserved and the fossa nasalis is filled with matrix.

**Structures on ventral surface:** The shape of the premaxilla in BMNH R.8432 seems to show a slight pinching, but the figures of GSI 17255 show no pinching. There is a slight midline concavity not defined posteriorly, but sloping dorsally into the apertura narium interna, similar to that seen in *Bairdemys venezuelensis*. There are no accessory ridges. The foramen praepalatinum is present on the left side. Only a small part of the labial ridge is present in either skull. It shows a low, blunt edge as is present on the maxillary labial ridge.

MAXILLA

**Preservation:** Both maxillae are present in GSI 17255 and BMNH R.8432. In BMNH R.8432 the labial ridges are slightly damaged and the posteroventral margin is broken. In GSI 17255 the breakage and missing areas are more extensive.

**Contacts of vertical plate:** The maxilla as preserved in *Shweboemys* contacts the premaxilla anteromedially, the jugal posterodorsally, and the prefrontal anterodorsally.

**Structures of vertical plate:** The ventral margin of the orbital rim is formed by the maxilla and is a relatively sharp ridge, as in all other subtribe Stereogenyina except *Lemurchelys*. There is no remnant of possible cheek emargination.

**Contacts of horizontal plate:** The horizontal plate of the maxilla contacts the premaxilla anteromedially, the palatine posteromedially, and the jugal posterolaterally.

**Structures of horizontal plate:** The triturating surface in *Shweboemys*, as in *Stereogenys*, has parallel medial margins forming the cleft-shaped apertura narium interna. However, the length of the secondary palate is shorter in *Lemurchelys* than in the other two genera. There is a slight convexity on the maxilla in *Shweboemys*, similar to that in *Lemurchelys*. The maxilla in *Shweboemys* is relatively thick and swollen as in *Lemurchelys*, in contrast to the thin and narrow maxilla in *Latentemys* and *Cordichelys*.

VOMER

It can be determined that there is no vomer in *Shweboemys*.

PALATINE

**Preservation:** Both palatines are present in GSI 17255 and BMNH R.8432. In both skulls the bones are damaged posteriorly but intact anteriorly.

**Contacts:** The palatine contacts the maxilla anterolaterally and the pterygoid posteriorly. There is a very slight midline contact with the basisphenoid in BMNH R.8432, separating the pterygoids on the midline, as in *Stereogenys* but no other subtribe Stereogenyina.

**Structures on ventral surface:** The palatine is longer than the maxilla in *Shweboemys, Brontochelys,* and *Stereogenys*. The palatine surface is slightly concave, as in *Latentemys*

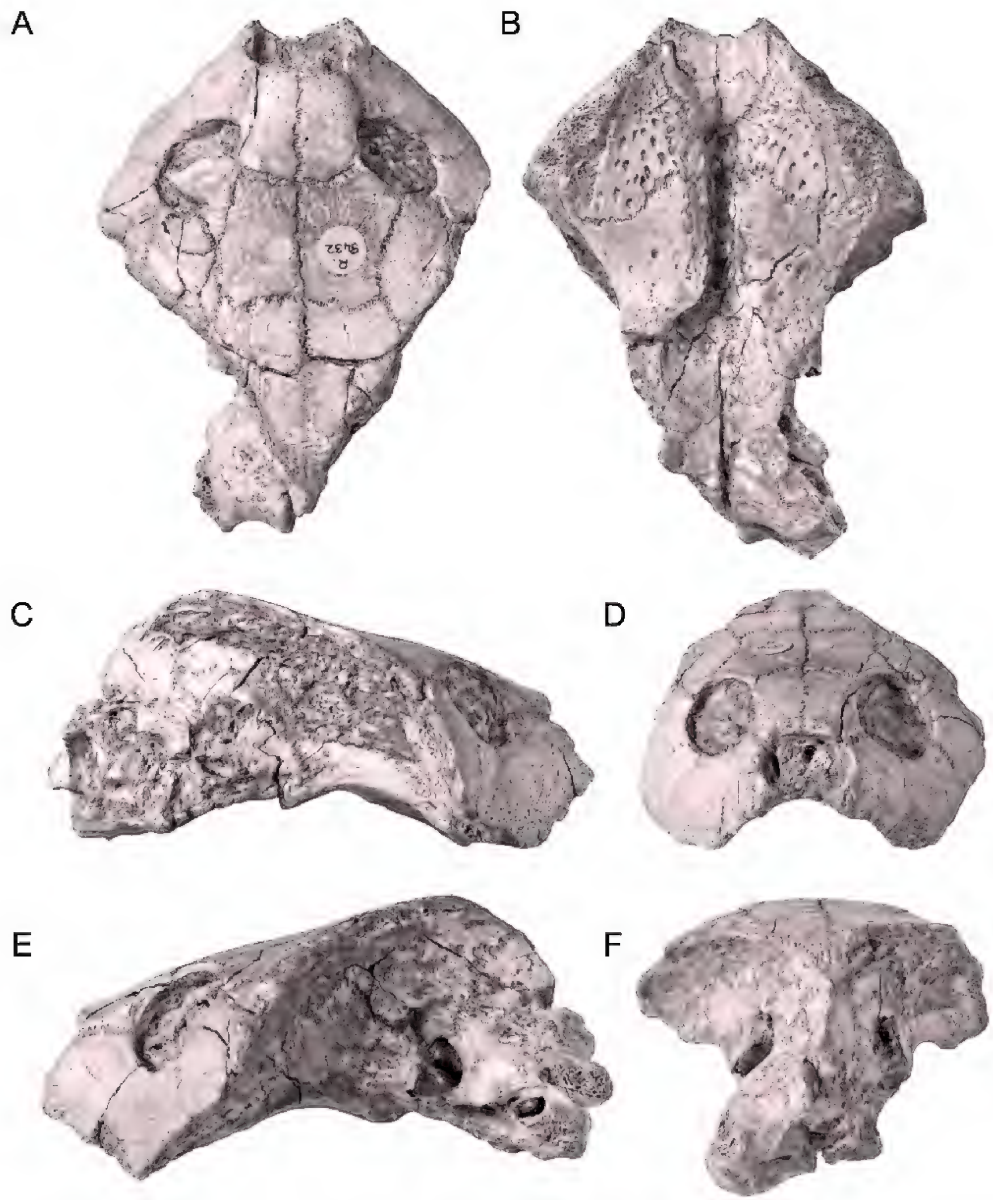


Fig. 73. *Shweboemys pilgrimi* Swinton, 1939. BMNH R.8432. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [F. Ippolito, del.]

and *Cordichelys*, but not as deep as in *Bairdemys venezuelensis*.

QUADRATE

**Preservation:** Only the medialmost contact area of the left quadrate remains in BMNH R.8432. None of the cheek or skull roof contacts remain. None of the quadrate is apparent in GSI 17255.

**Contacts:** The only remaining quadrate contacts are with the pterygoid anteromedially, the basisphenoid medially, the basioccipital posteromedially, and what seems to be the prootic medially.

**Structures:** The medial part of the incisura columellae auris is present on the left side of BMNH R.8432. At this position it is an oval tunnel formed mostly by the quadrate and

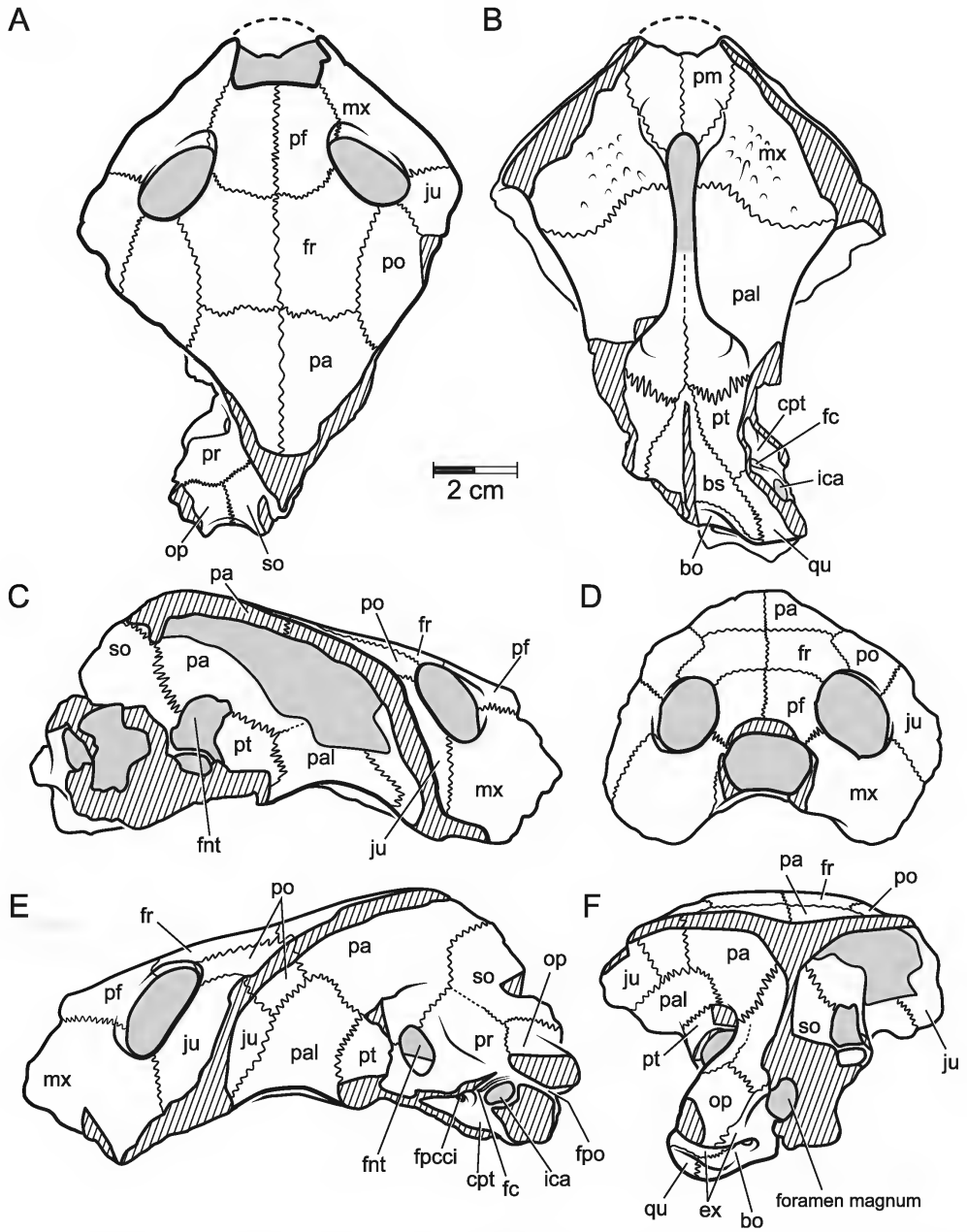


Fig. 74. *Shweboemys pilgrimi* Swinton, 1939. BMNH R.8432. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [F. Ippolito, del.]

probably the prootic, although sutures are unclear.

PTERYGOID

**Preservation:** The anterior and medial portions of both pterygoids are present in BMNH R.8432. Only anterior portions seem to be present in GSI 17255.

**Contacts on ventral surface:** The pterygoid contacts the palatine anteriorly, the basisphenoid posteromedially, and the quadrate posterolaterally. In *Shweboemys*

there is no midline contact with the other pterygoid.

**Structures on ventral surface:** The processus trochlearis pterygoidei is broken away on both *Shweboemys* specimens. The posterior portion of the cavum pterygoidei is visible on the left side of BMNH R.8432, and is floored by the pterygoid. There is no sign of a foramen palatinum posterius. See Quadrate for cavum pterygoidei description.

**Contacts on dorsal surface:** The contacts of the pterygoid in BMNH R.8432 at the base of the processus trochlearis pterygoidei are with the palatine anteriorly and the parietal dorsally. The contacts of the crista pterygoidea are unclear due to matrix and the only contact visible is with the parietal anterodorsally.

**Structures on dorsal surface:** The sulcus palatinopterygoideus and its associated septum orbitotemporale are formed in BMNH R.8432 by the postorbital, parietal, pterygoid, and the unusually large palatine. As in the other subtribe Stereogenyina, the foramen nervi trigemini in BMNH R.8432 is formed by the parietal anterodorsally, the prootic dorsolaterally, and the pterygoid ventrally.

SUPRAOCCIPITAL

**Preservation:** Only a small portion of the base of the supraoccipital is preserved in BMNH R.8432, the crista supraoccipitalis is broken away. The supraoccipital seems to be missing in GSI 17255.

**Contacts:** As in other subtribe Stereogenyina the supraoccipital contacts the parietals dorsally and anteriorly, the prootic anterolaterally, the opisthotic posterolaterally, and the exoccipitals posteroventrally.

**Structures:** Although most of the structure is broken away, the base of the crista in BMNH R.8432 is not deep as in *Lemurchelys*.

EXOCCIPITAL

**Preservation:** Most of the left exoccipital is present in BMNH R.8432. The break is just lateral to the condylus occipitalis and that structure is missing. The exoccipital is missing in GSI 17255.

**Contacts:** The exoccipital in *Shweboemys* contacts the supraoccipital dorsally, the opisthotic laterally, and the basioccipital ventrally.

**Structures:** The foramina nervi hypoglossi are combined into a single recessed opening, as seen in *Lemurchelys*. The foramen jugulare posterius is closed by bone, which seems to include the opisthotic and basioccipital.

BASIOCCIPITAL

**Preservation:** The left part of the basioccipital in BMNH R.8432 is mostly present, but it is broken just lateral to the midline, missing the condylus occipitalis. The basioccipital is missing in GSI 17255.

**Contacts:** The basioccipital in *Shweboemys* contacts the basisphenoid anteriorly, the quadrate laterally, and the exoccipitals posterodorsally.

**Structures:** Compared with forms like *Latentemys* and *Cordichelys*, BMNH R.8432 has a tuberculum basioccipitale, similar to the one in those genera.

PROOTIC

**Preservation:** Most of the left prootic in BMNH R.8432 is present; its lateral margins are broken edges, however. The prootic seems to be missing in GSI 17255.

**Contacts:** The prootic in *Shweboemys* contacts the parietal dorsomedially, the quadrate laterally, the supraoccipital posterodorsally, the pterygoid ventrally, the basisphenoid ventrally, and the opisthotic posteriorly, as in other podocnemidids.

**Structures:** The prootic in *Shweboemys* is very similar to that bone in the other subtribe Stereogenyina. The medial edge of the foramen stapedio-temporale is preserved. The prootic forms part of the foramen cavernosum in the roof of the cavum pterygoidei, and this can be seen in section on the left side of BMNH R.8432. The canalis cavernosus is visible dorsal to the incisura columellae auris.

OPISTHOTIC

**Preservation:** The medial part of the left opisthotic is preserved in BMNH R.8432. The opisthotic is missing in GSI 17255.

**Contacts:** Enough of the contacts can be made out in BMNH R.8432 to see that they are as in other podocnemidids: the supraoccipital anteromedially, the prootic anteriorly, the quadrate anterolaterally, and the exocci-

pital posteromedially. The squamosal contact is not preserved.

**Structures:** The opisthotic forms the lateral wall of the foramen jugulare posterius and, probably, the medial wall of the fenestra postotica, although the latter opening is not preserved.

BASISPHENOID

**Preservation:** The basisphenoid in BMNH R.8432 is cracked down its midline, with the left portion complete and the right portion lacking its distal end. The basisphenoid seems to be missing in GSI 17255, although its anteriormost margin may be present. We don't know.

**Contacts on ventral surface:** The basisphenoid contacts the pterygoids anterolaterally, the basioccipital posteriorly, the prootic dorsolaterally (within the cavum pterygoidei), and the quadrate laterally. The basisphenoid in BMNH R.8432 barely contacts the palatines to separate the pterygoids on the midline. The degree of contact varies from side to side; on the left side it is longer than on the right side. This contact differs from that in *Stereogenys*, which has a broad contact with palatines and widely separates the pterygoids. *Cordichelys* has a basisphenoid that approaches the palatines and separates the pterygoids for most of their length.

**Structures on ventral surface:** The basisphenoid shape in *Shweboemys* is roughly as wide as long, similar to that in *Bairdemys venezuelensis* and *Cordichelys*. This differs from the very short basisphenoid seen in *Brontochelys* and *Lemurchelys*. In BMNH R.8432 the foramen anterius canalis carotici interni can be seen in the basisphenoid on the left side where the cavum pterygoidei is broken away laterally exposing the medial wall.

*Stereogenys*
Figures 75–82

PREFRONTAL

**Preservation:** In DPC 4120 both prefrontals are complete except for parts of the ventral processes. BMNH R.3007, BMNH R.3190, and AMNH 14736 have the prefrontal area preserved but no visible sutures and no internal information. BMNH R.3189 has both prefrontals preserved, pitted on the dorsal surface but some sutures visible. BMNH R.3191 preserves none of the prefrontal.

**Contacts:** In *Stereogenys* the prefrontal contacts the other prefrontal on the midline, the maxilla anteroventrolaterally, the frontal posteriorly, and the palatine ventrally, as in the other subtribe Stereogenyina.

**Structures:** The dorsal plate in *Stereogenys* is flat with an anteriorly protruding dorsal margin of the apertura narium externa that, based on the relatively complete nose of AMNH 14736, does not overlap the premaxillae in dorsal view. The prefrontal forms the anterodorsal margin of the orbital rim, as in the other subtribe Stereogenyina.

FRONTAL

**Preservation:** In DPC 4120 the right frontal is complete, but the left one lacks its lateral margin. BMNH R.3007 and AMNH 14736 have the frontal area preserved, slightly crushed, and no visible sutures, no internal information. BMNH R.3189 has both frontals preserved, pitted and crushed on the dorsal surface, but some sutures are visible. BMNH R.3190 has both frontals preserved, pitted and crushed on the dorsal surface, with no sutures visible. BMNH R.3191 preserves none of the actual frontal bone, but probably has some of the posteroventral imprint of the frontal sulcus olfactorius.

**Contacts and structures:** The frontal in *Stereogenys* contacts the other frontal on the midline, the prefrontal anteriorly, the postorbital posterolaterally, and the parietal posteriorly. On the ventral surface the posteroventral process of the frontal contacts the dorsal process of the palatine. On the ventral surface, the frontal forms the sulcus olfactorius, which can be seen in both endocasts (figs. 79, 80, 82).

PARIETAL

**Preservation:** In DPC 4120 both parietals lack the dorsal plate over the fossa temporalis and preserve only the sections over the cavum cranii. The ventral portions are complete. BMNH R.3007 has the parietal area preserved, slightly crushed, and no visible sutures. The right parietal is complete; the left is broken laterally. AMNH 14736 has the parietal area partially preserved but badly

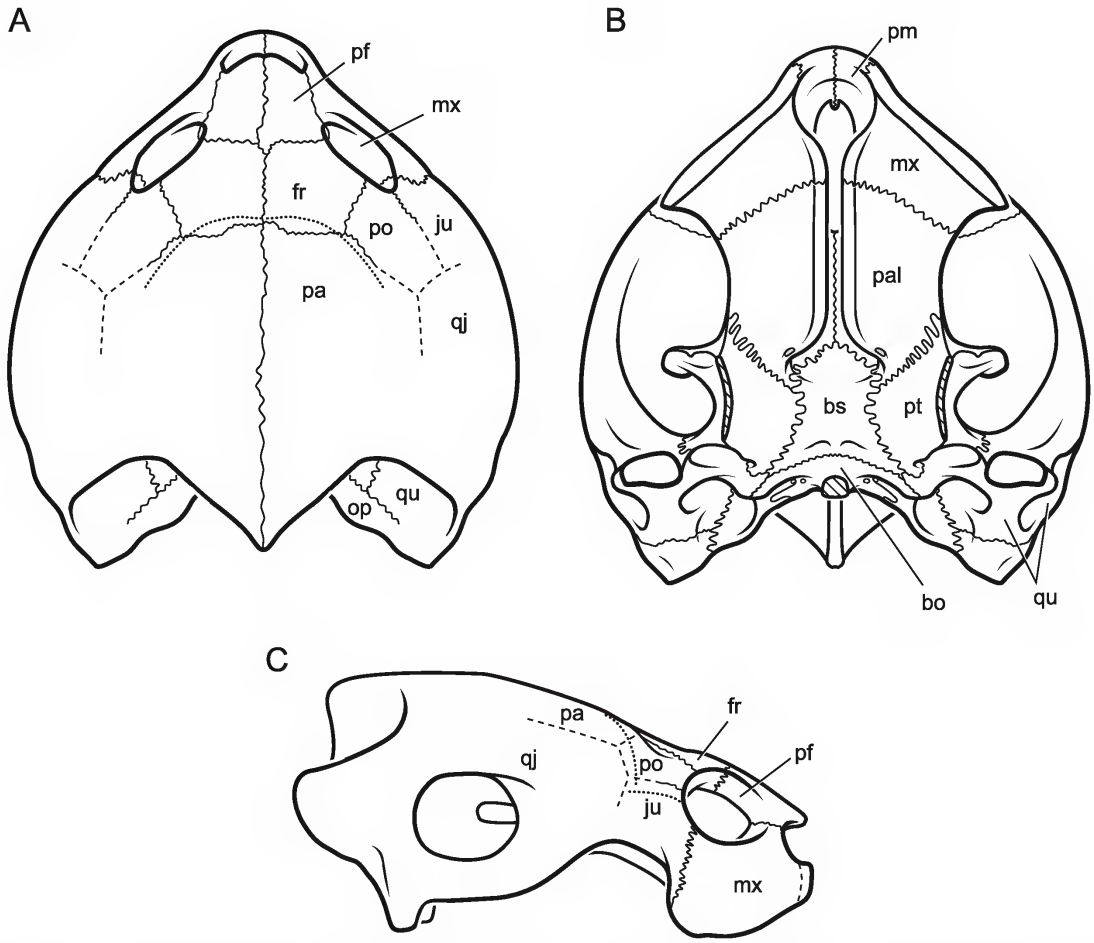


Fig. 75. *Stereogenys cromeri* Andrews, 1901. Partially restored skull based on DPC 4120, BMNH R.3190, BMNH R.8442, BMNH R.3906, BMNH R.3189, BMNH R.3191. **A,** dorsal; **B,** ventral; **C,** lateral. [F. Ippolito, del.]

eroded. BMNH R.3189 has both parietals present anteromedially, pitted on the dorsal surface, but some sutures are visible; they lack the dorsal plate over the fossa temporalis and preserve only the sections over the cavum cranii. BMNH R.3190 has portions of both parietals preserved, pitted and crushed on the dorsal surface, with no sutures visible. The right one lacks the dorsal plate over the fossa temporalis, but the left one has most of the skull roof, slightly crushed, with no sutures. BMNH R.3191 preserves only a small part of the posterolateral vertical wall of the parietal on the left side. It also preserves the endocast of the cavum cranii, largely formed by the parietal.

**Contacts of dorsal plate:** Based on the well-preserved DPC 4120, the contacts can be seen, but DPC 4120 does not have the skull roofing elements preserved posteriorly, and the other specimens that are complete do not show sutures. As preserved, the parietal in *Stereogenys* contacts the other parietal on the midline, the postorbital anterolaterally, and the frontal anteriorly. There is probably a quadratojugal contact posterolaterally, and BMNH R.3190 shows a crack in the right place, but the material really is too poorly preserved to be sure. What can be determined from the material is that *Stereogenys* had a fully roofed skull with only a slight emargination exposing the posterior edge of the otic

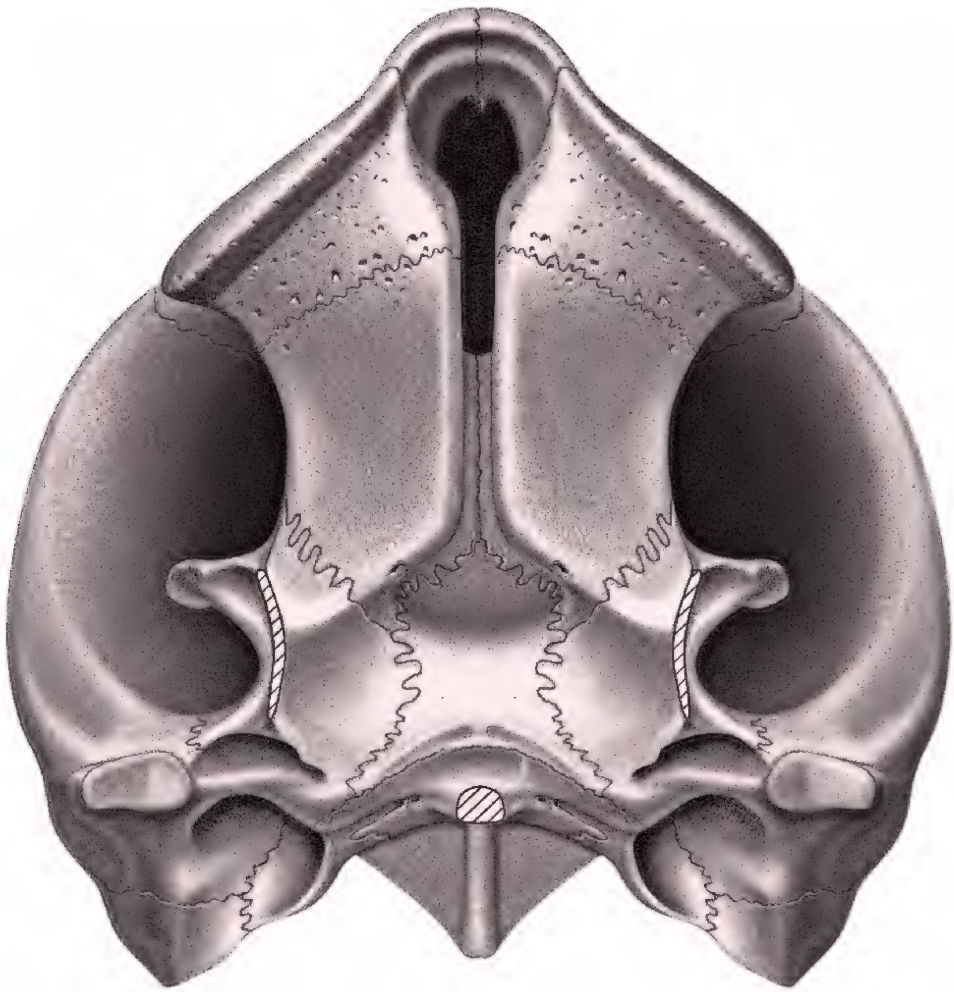

Fig. 76. *Stereogenys cromeri* Andrews, 1901. Partially restored ventral view based primarily on DPC 4120, with additions from BMNH R.3190, BMNH R.8442, and BMNH R.3191. **A,** dorsal; **B,** ventral; **C,** lateral. [F. Ippolito, del.]

chamber in dorsal view, much as in *Bairdemys venezuelensis*.

**Contacts and structures of processus inferior parietalis:** The processus can be seen in DPC 4120 and the endocast made from it. It shows that the contacts in *Stereogenys* are with the palatine anteroventrally, the pterygoid ventrally, the prootic posteroventrally, and the supraoccipital posteriorly. The processus inferior parietalis forms the medial wall of the sulcus paltinopterygoideus. In the lateral wall, the parietal contacts the postorbital anteriorly, the palatine anteroventrally, and the pterygoid posteroventrally (fig. 78). The foramen nervi trigemini is formed by the parietal anterodorsally, prootic dorsolaterally, and pterygoid ventrally.

JUGAL

**Preservation:** In DPC 4120 none of the left jugal remains. The right jugal has its medial process and the anterior portion of the lateral plate. BMNH R.3007 has the jugal area preserved on both sides, slightly crushed, with possible sutures, but sutures appear the same as cracks. Both jugals are broken posteriorly. AMNH 14736 has the jugal area partially preserved but badly eroded. BMNH R.3189 has both jugals present medially, pitted and poorly preserved, with only the

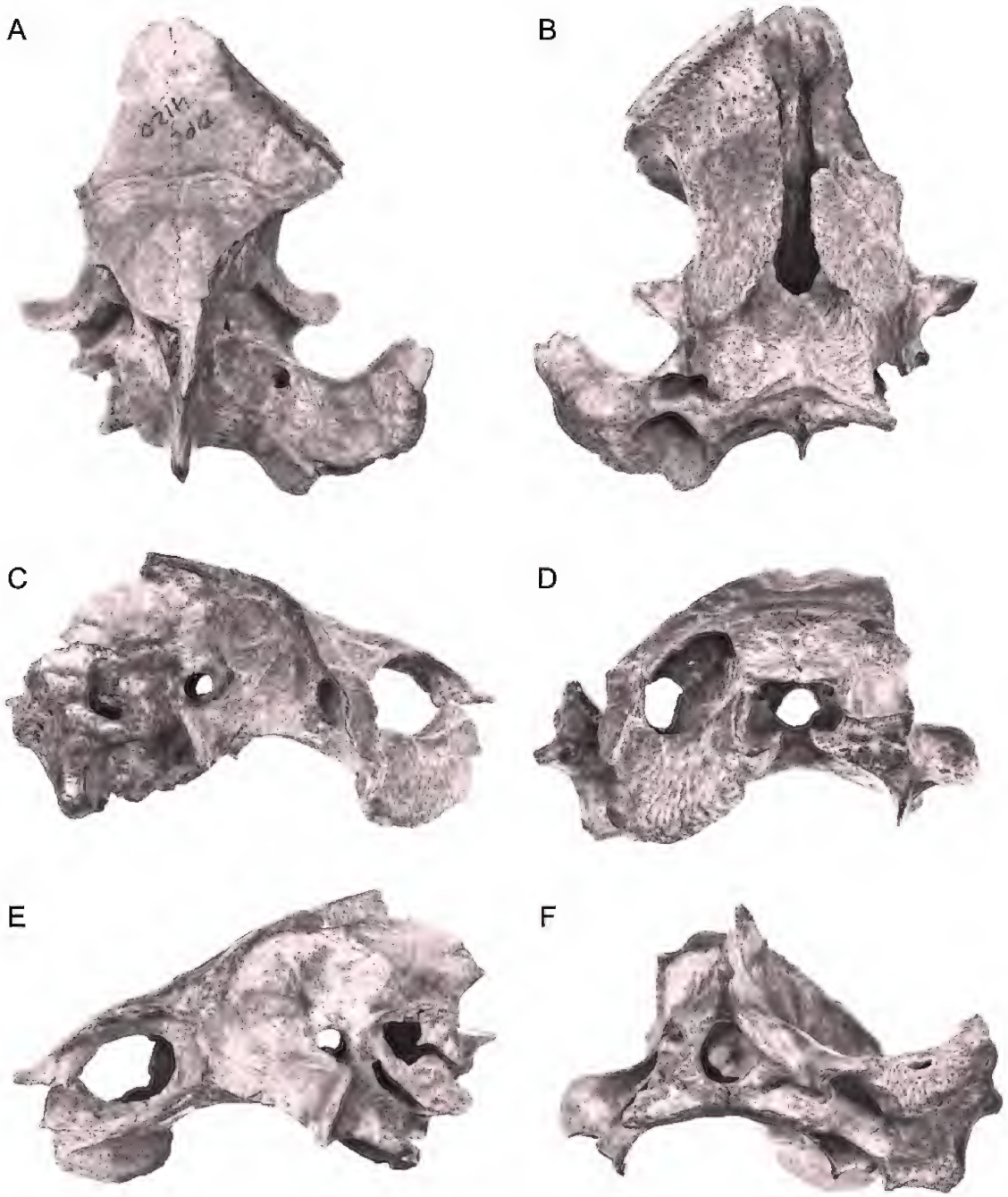


Fig. 77. *Stereogenys cromeri* Andrews, 1901. DPC 4120. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [E. Heck, del.]

medial process present. BMNH R.3190 has portions of both jugals preserved, pitted and crushed on the dorsal surface, with no sutures visible. BMNH R.3191 preserves none of the jugal.

**Contacts and structures of lateral plate:** The posterior extent of the jugal is not known in *Stereogenys*, but its known contacts are with the maxilla anteroventrally and the postorbital dorsally. The extent of the cheek

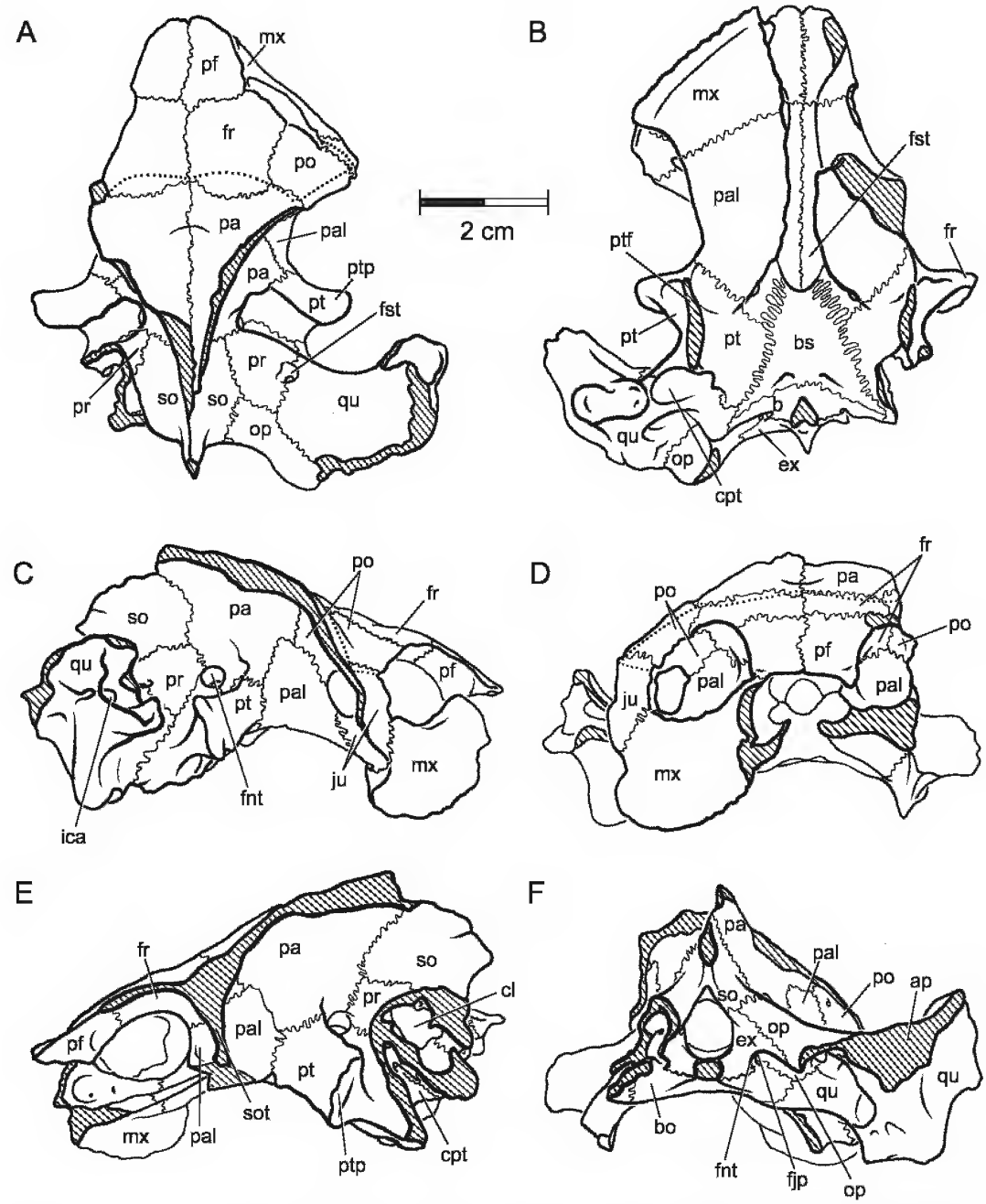


Fig. 78. *Stereogenys cromeri* Andrews, 1901. DPC 4120. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. [M. Rightmyer, del.]

emargination in *Stereogenys* is seen in BMNH 3190, and it is nearly absent—less than in *Bairdemys venezuelensis*.

**Contacts of medial process:** In the anterior surface of the septum orbitotemporale in *Stereogenys*, the jugal contacts the maxilla anteriorly and laterally and the palatine medially. In the posterior surface of the septum orbitotemporale, the jugal contacts the postorbital dorsomedially, the palatine

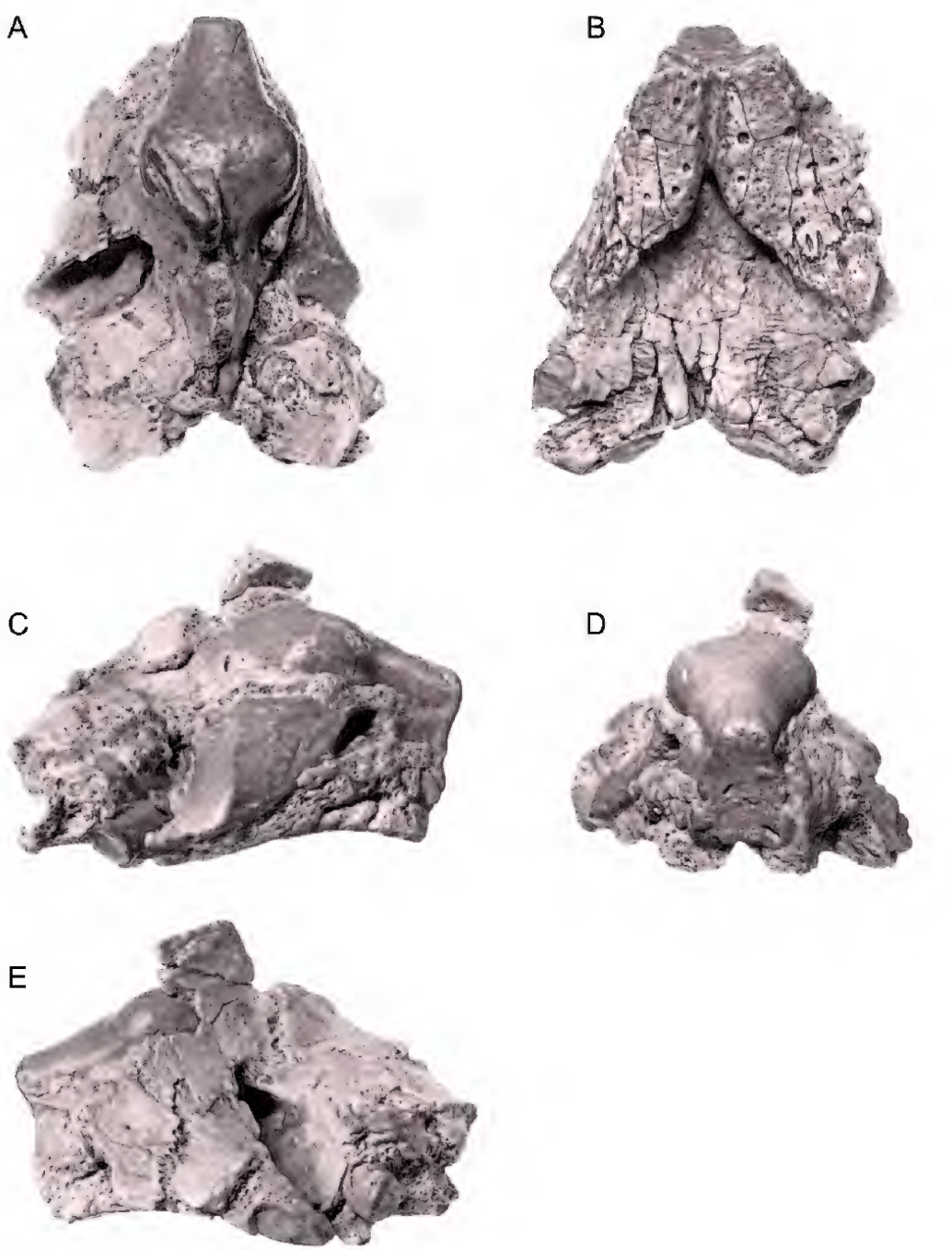


Fig. 79. *Stereogenys cromeri* Andrews, 1901. BMNH R.3191. Partial braincase and palate. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral. [E. Heck, del.]

ventromedially, and the maxilla ventrally. The usual pterygoid contact is prevented by a large dorsal process of the palatine that reaches the postorbital. This condition is also in *Shweboemys* but not in any other subtribe Stereogenyina.

**Structures of medial process:** The jugal in *Stereogenys* participates in the formation of

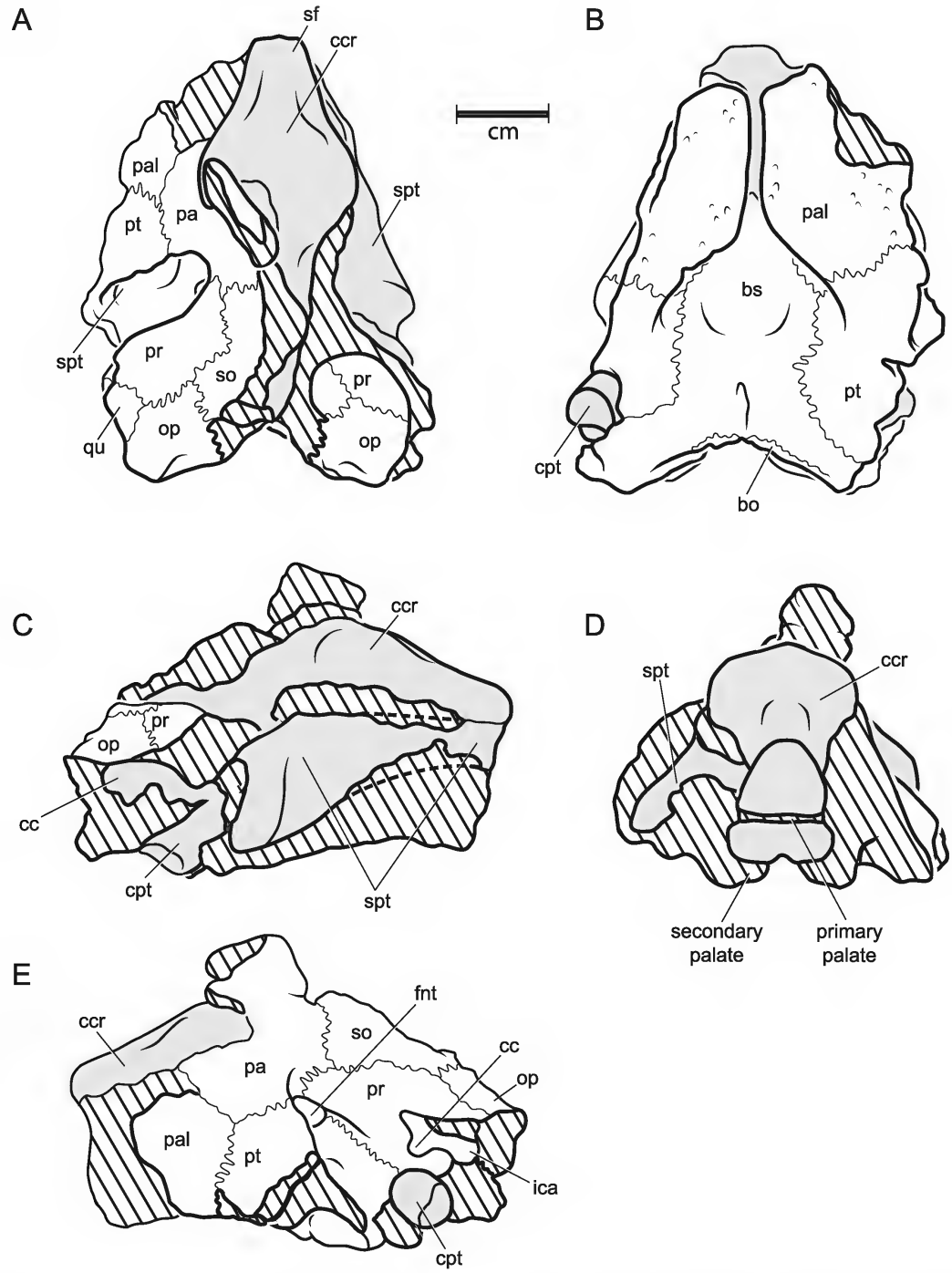


Fig. 80. *Stereogenys cromeri* Andrews, 1901. BMNH R.3191. Partial braincase and palate. **A,** dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral. [C. Wilson, del.]

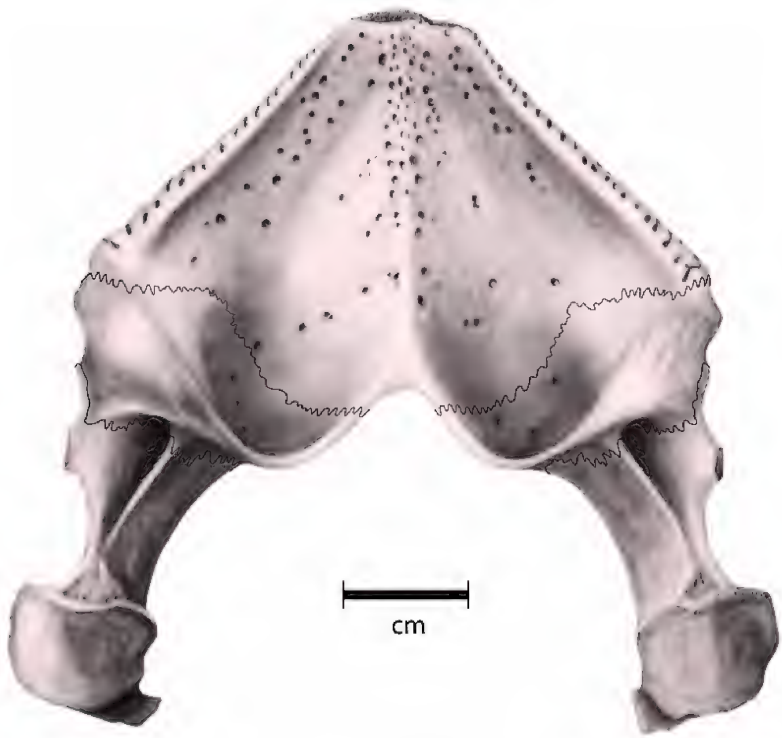


Fig. 81. ? *Stereogenys cromeri* Andrews, 1901. University of Michigan 161. Lower jaw. [N. Hennelly, del.]

the septum orbitotemporale and its enclosed space, the sulcus palatinopterygoideus (fig. 80). The septum orbitotemporale of the subtribe Stereogenyina, as seen in *Stereogenys*, especially the endocasts (figs. 79, 80, 82), is a relatively thick wall, thicker and longer than the processus inferior parietalis, the wall that actually encloses the cavum cranii proper. Presumably the thick wall and large sulcus are associated with the secondary palate.

QUADRATOJUGAL

**Preservation:** The quadratojugal in *Stereogenys* is not preserved in DPC 4120. BMNH R.3007 has the quadratojugal area preserved on the right side, slightly crushed, and no apparent sutures. AMNH 14736 has the quadratojugal area partially preserved on the right side. BMNH R.3189 lacks both quadratojugals. Some of both quadratojugals are probably present in BMNH R.3190, but the areas are poorly preserved and lack sutures. BMNH R.3191 preserves none of the quadratojugal.

**Contacts and structures:** The few specimens that preserve the area of the quadratojugal have no sutures. A cheek emargination is absent.

SQUAMOSAL

**Preservation:** The squamosal in *Stereogenys* is not preserved in DPC 4120. BMNH R.3007 has the squamosal area preserved on both sides, slightly crushed, without sutures. The right side is more complete than the left. AMNH 14736 has both squamosals preserved but eroded. BMNH R.3189 lacks both squamosals. In BMNH R.3190 the right squamosal is probably complete, although poorly preserved, with no sutures, and a portion of the left is probably present. BMNH R.3191 preserves none of the squamosal.

**Contacts and structures:** None of the specimens of *Stereogenys* with the squamosal preserved have sutures. The shape of the squamosal is similar to that in *Latentemys*, there is no vertical flange as seen in *Bairdemys*.

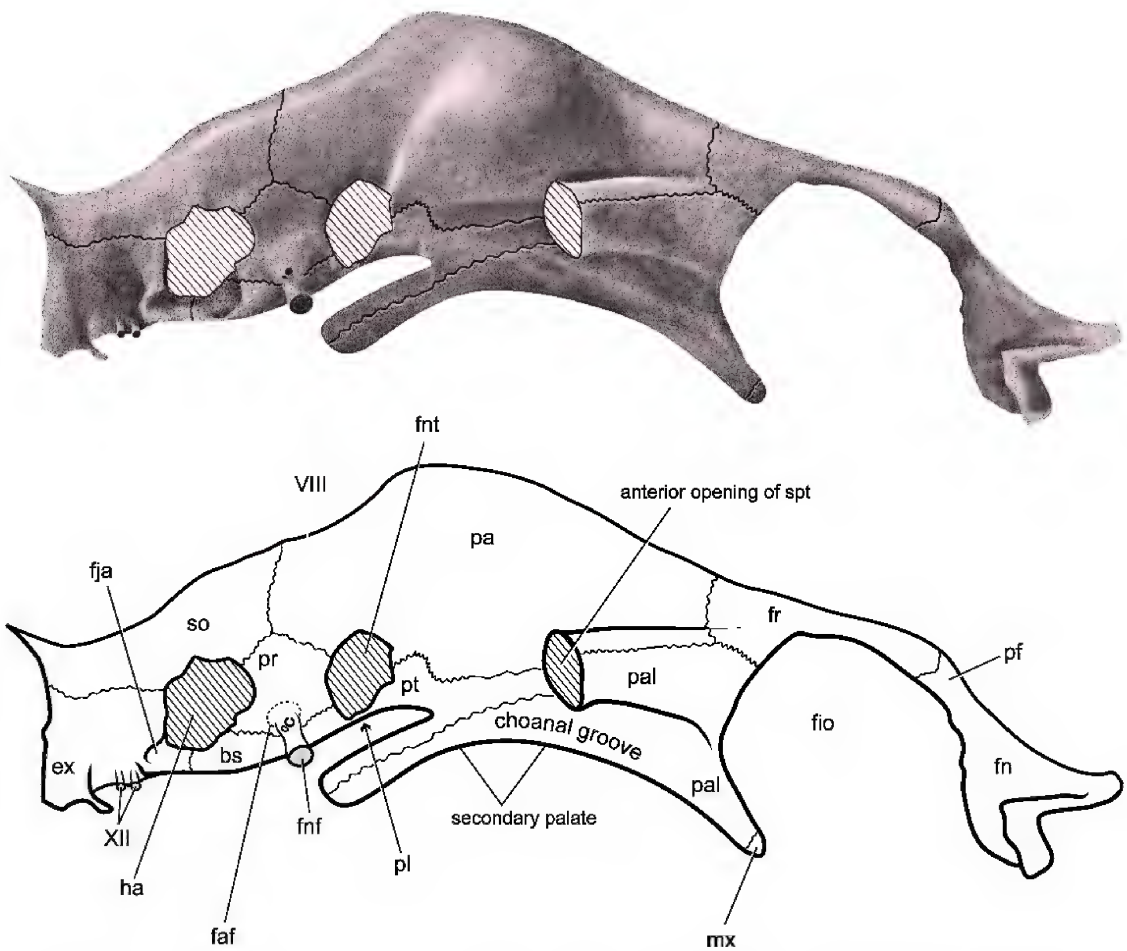


Fig. 82. *Stereogenys cromeri* Andrews, 1901. DPC 4120. Endocast. [L. Starin, F. Ippolito, del.]

POSTORBITAL

**Preservation:** The left postorbital in *Stereogenys* is missing in DPC 4120, but the right one preserves its medial process and most of the lateral plate. BMNH R.3007 has the postorbital area preserved on both sides, slightly crushed, and lacking sutures. AMNH 14736 has the postorbital area preserved but eroded. BMNH R.3189 probably has portions of both postorbitals in the orbital rims, but sutures are not visible. On the left side of BMNH R.3190 the postorbital area is preserved, but there are no sutures. BMNH R.3191 preserves none of the postorbital.

**Contacts of lateral plate:** The posterior part of the postorbital is missing in DPC 4120. The contacts as preserved in *Stereogenys* are with the frontal anteromedially, the jugal ventrally, and the parietal posteromedially. The possible quadratojugal contact is not determinable.

**Structures of lateral plate:** As preserved, the postorbital of *Stereogenys* agrees with *Bairdemys* in the formation of the orbital rim and the absence of a temporal emargination.

**Contacts of medial process:** In the anterior surface of the septum orbitotemporale in *Stereogenys* the postorbital contacts the frontal dorsomedially, the palatine ventrally, and the jugal ventrolaterally. In the posterior wall of the septum orbitotemporale, the postorbital contacts the parietal dorsomedially, the jugal ventrolaterally, and the palatine ventrally. The usual pterygoid contact is prevented by the large palatine from reaching the parietal and postorbital, as in *Shweboemys*.

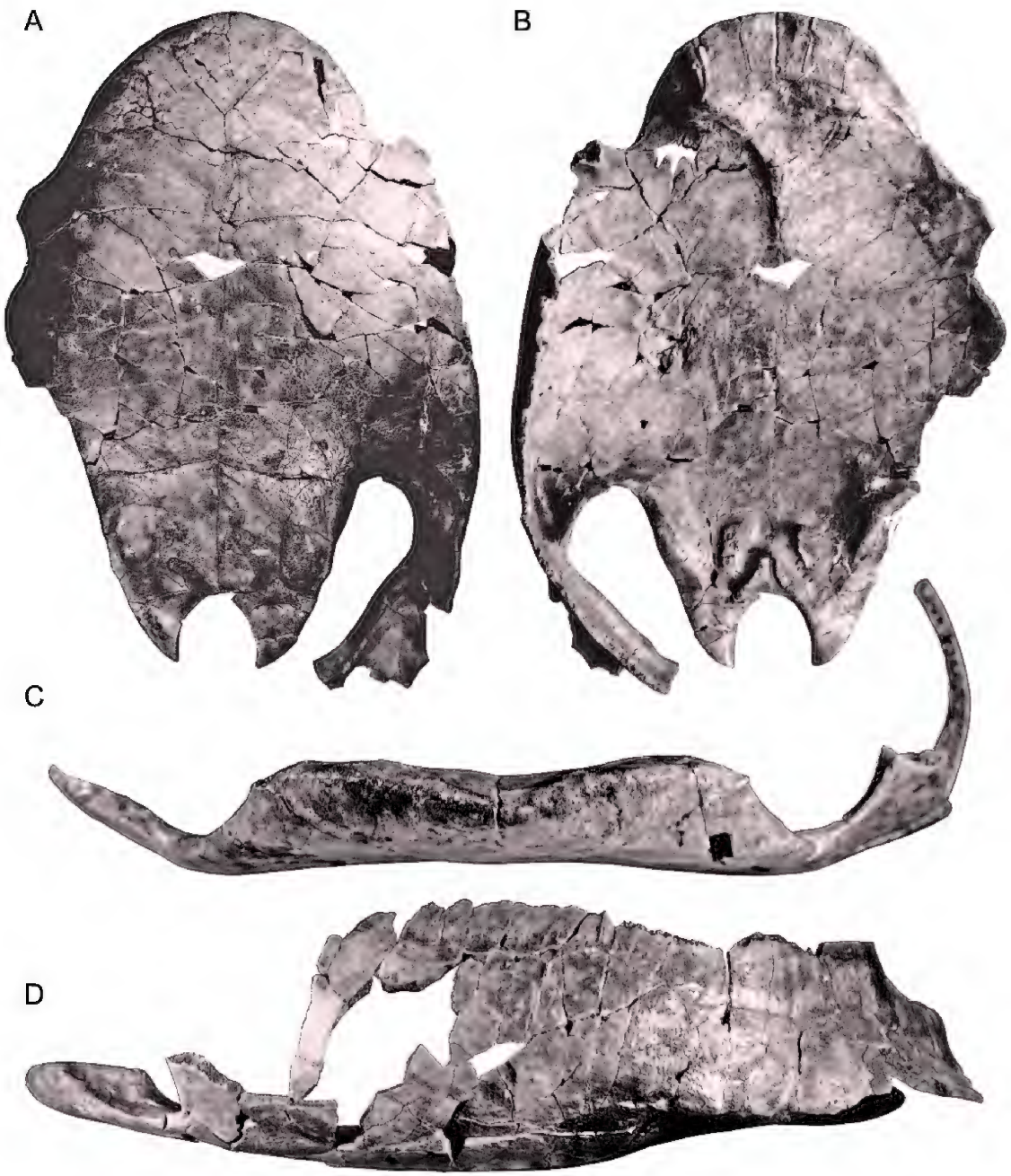


Fig. 83. *Albertemys woodi,* n. gen. et sp. AMNH 5088. Plastron and partial carapace. **A,** dorsal; **B,** ventral; **C,** anterior; **D,** left lateral. [R. Wood, del.]

**Structures of medial process:** The postorbital in *Stereogenys* is not actually exposed within the sulcus palatinopterygoideus, although it forms part of the septum orbitotemporale on the outside of the structure. This is also seen in *Latentemys,* but the material of other subtribe Stereogenyina is not well enough preserved or prepared to allow further comparisons.

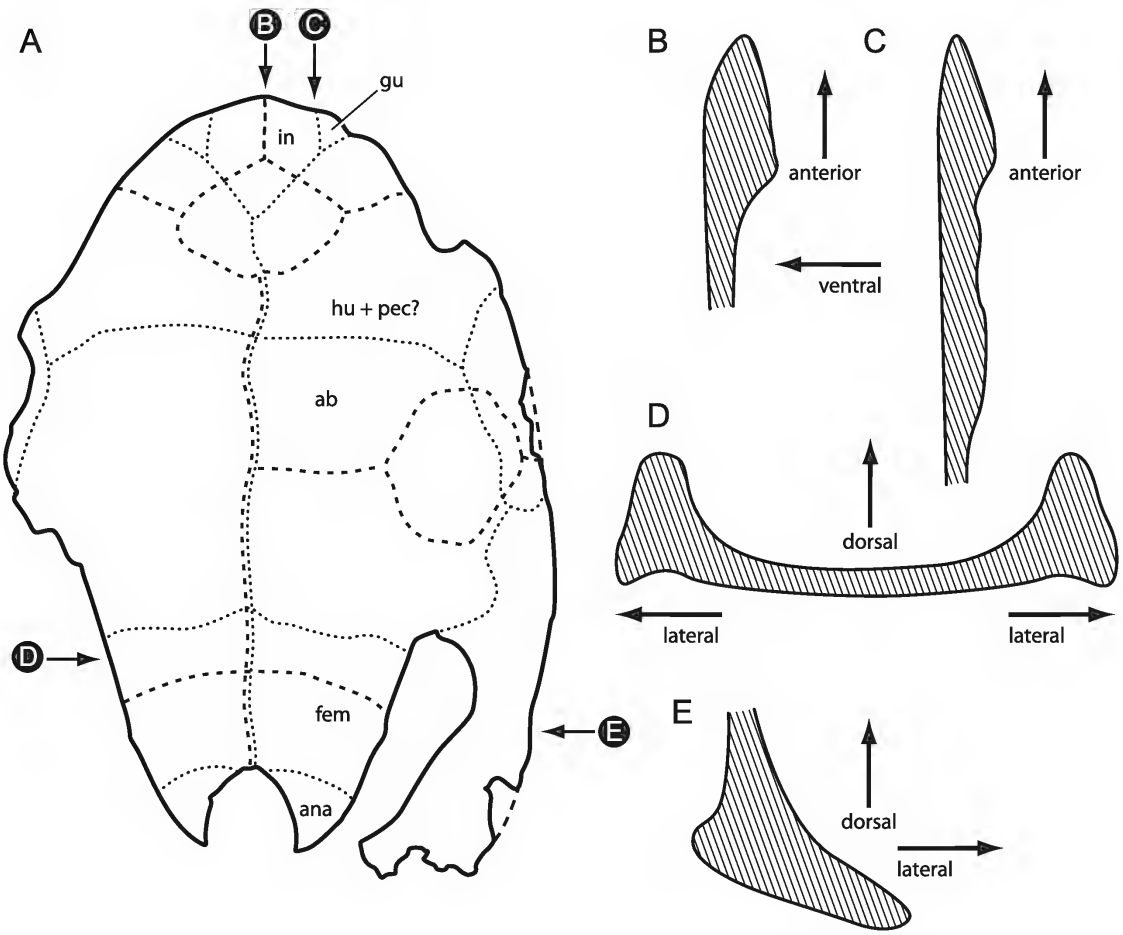


Fig. 84. *Albertemys woodi,* n. gen. et sp. AMNH 5088. Plastron and partial carapace. **A,** ventral view of plastron; **B, C, D, E,** cross sections at positions indicated. [R. Wood, C. Facella, del.]

PREMAXILLA

**Preservation:** The premaxilla in *Stereogenys* is not preserved in DPC 4120. BMNH R.3007 lacks the premaxilla; the apparent presence of them in Andrews (1906: fig. 95) shows only the underside of the skull roof, which appears to be premaxillae. AMNH 14736 has both premaxillae preserved but eroded. BMNH R.3189 has both premaxillae present; they are not well preserved and are crushed dorsomedially. BMNH R.3190 has both premaxillae, complete but partially deformed. BMNH R.3191 preserves none of the premaxilla.

**Contacts and structures:** DPC 4120 has no premaxilla but shows a sutural margin along the anteromedial edge of the right maxilla. BMNH R.3190 has the best-preserved premaxillae, but they show no definite sutures. There is a relatively thick labial ridge in *Stereogenys* that forms the apex of an anterior projection of the skull, in contrast to *Bairdemys venezuelensis.* The triturating surface of the premaxilla has a low accessory ridge that parallels the labial ridge.

MAXILLA

**Preservation:** In DPC 4120 the left maxilla is missing. The right one is nearly complete but lacks its anteromedial edge and a small portion of its anterior edge. BMNH R.3007 has the maxilla preserved on both sides, slightly crushed, and showing sutures posteriorly (Andrews, 1906: pl. 25, fig. 2); dorsal and ventral surfaces are visible. AMNH 14736 has both maxillae preserved but

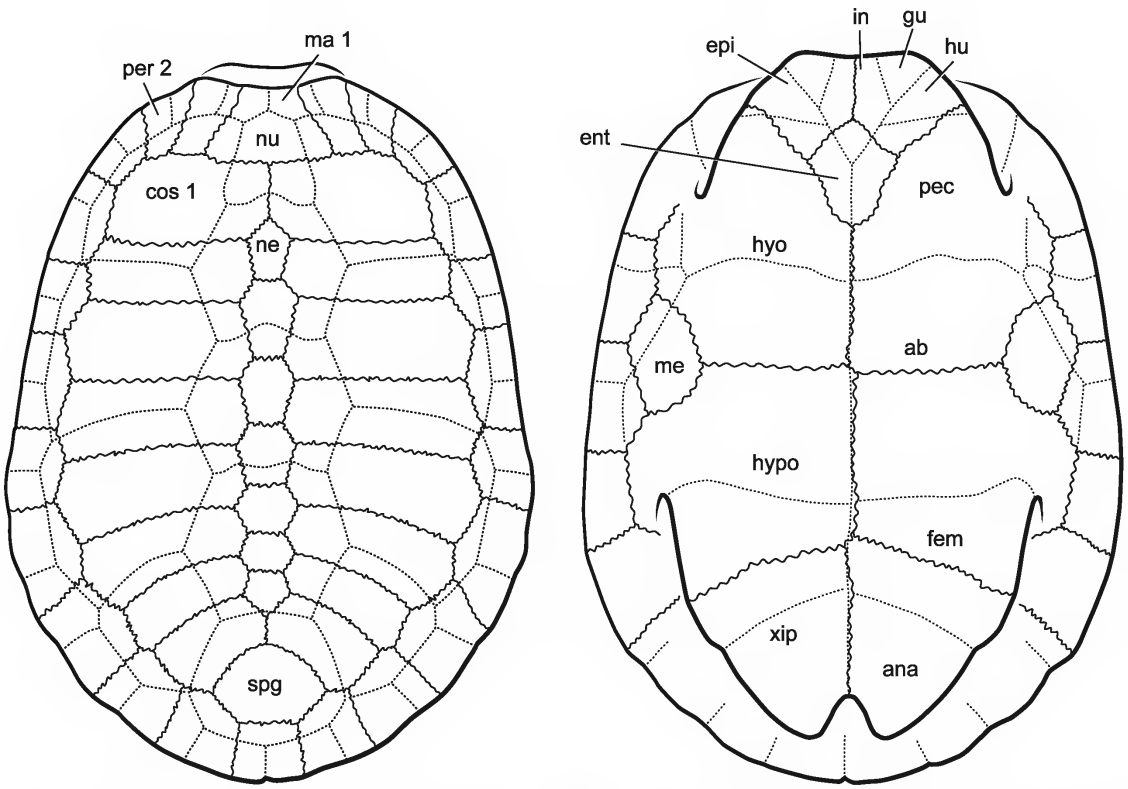


Fig. 85. *"Stereogenys" libyca* Andrews, 1903. Partially restored shell based on Andrews (1903: pl. 7, figs. A, B). [R. Wood, C. Wilson, del.]

eroded. BMNH R.3189 has both maxillae present; they are not well preserved and are crushed dorsomedially, although the left is better preserved and retains the labial ridge. BMNH R.3190 has both maxillae present, and relatively complete, except for posterior cracking and breakage. BMNH R.3191 preserves none of the maxilla.

**Contacts and structures of vertical plate:** The maxilla in *Stereogenys* contacts the premaxilla anteromedially, the jugal posterodorsally, and the prefrontal anterodorsally, as in the other subtribe Stereogenyina. There is either no cheek emargination or a very slight one, based on BMNH R.3190.

**Contacts of horizontal plate:** The contacts are with the premaxilla anteromedially, the palatine posteromedially, and the jugal posterolaterally.

**Structures of horizontal plate:** The maxilla forms the anterior third of the secondary palate characteristic of the subtribe Stereogenyina. It is much wider than in *Bairdemys* and lacks the convex swellings seen in *B. venezuelensis*. The labial ridge in *Stereogenys* is relatively low and thick, as in *Shweboemys* and *Brontochelys*, in contrast to the higher, narrower one in *Bairdemys*. The choanal passages can be seen in DPC 4120 and the endocast made from it. The passages are mostly in the palatine, but they begin anteriorly in the fossa nasalis, which is formed by the maxilla and premaxilla. The maxilla forms the lateral part of the fossa orbitalis; the orbital rim has a slight raised edge, lower than that seen in *Bairdemys venezuelensis*.

The maxillary (along with the palatine) postmortem crushing in some of the BMNH specimens led Andrews (1901: 442; 1906: 297) to suggest that *Stereogenys* may have had a completely closed palate, sutured on the midline. He did state that this was ambiguous, some specimens had a midline cleft and some seemed to be in contact. This was not clarified until Swinton (1939: 551; and later,

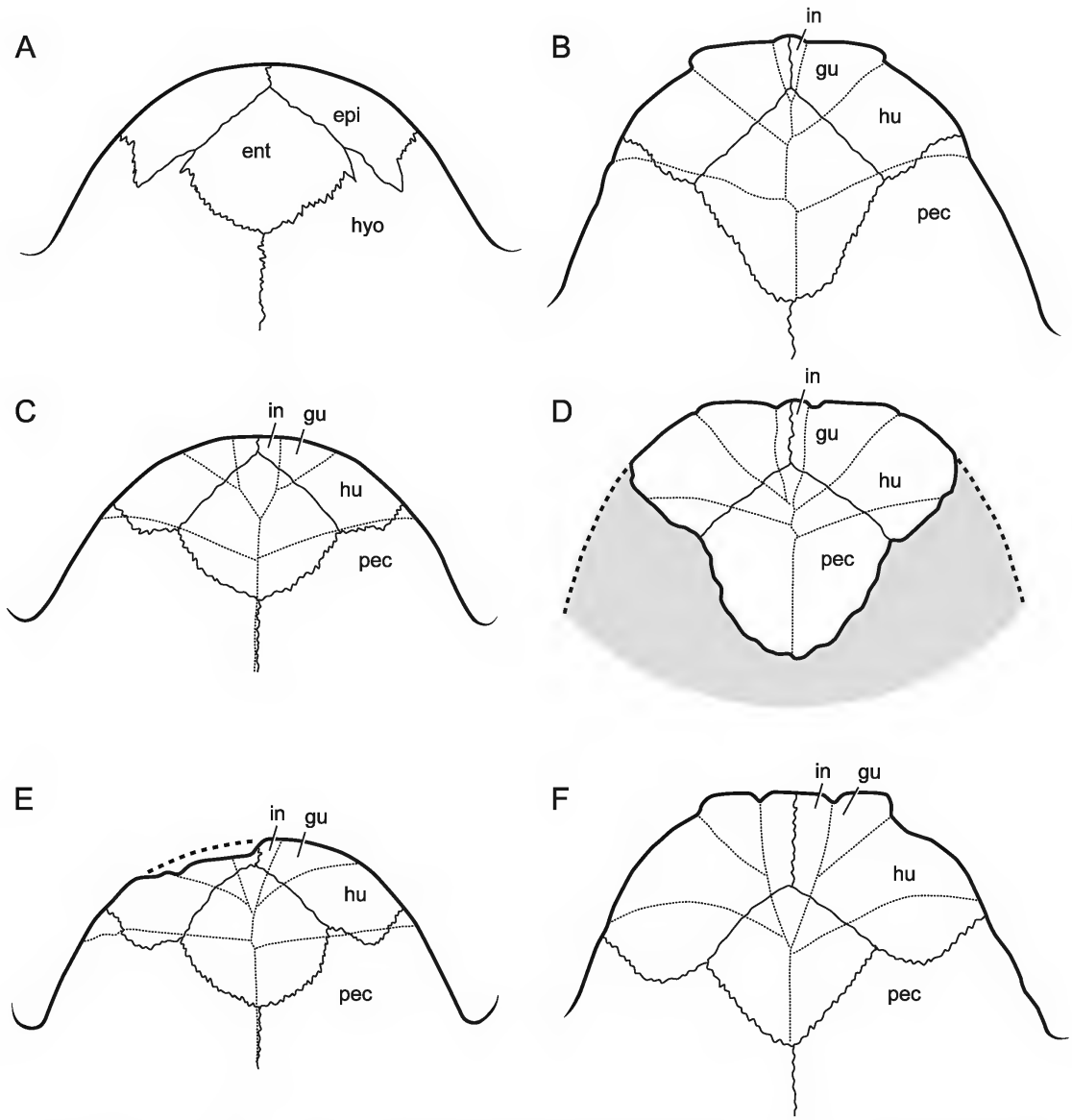


Fig. 86. Anterior lobes of Fayum podocnemidids. **A,** dorsal view of *Cordichelys antiqua,* n. gen. et sp., YPM 6205 (holotype); **B,** ventral view of *Neochelys fajumensis,* AMNH 5086; **C,** ventral view of *Cordichelys antiqua,* n. gen. et sp., YPM 6205 (holotype); **D,** ventral view of *Neochelys fajumensis,* AMNH 5093; **E,** ventral view of "*Podocnemis stromeri*" Reinach, 1903a, a synonym of *C. antiqua;* **F,** ventral view of *"Stereogenys" podocnemoides* Reinach, 1903b. Not to scale. [R. Wood, C. Wilson, del.]

Wood, 1970) recognized that both the better preserved *Shweboemys* as well as *Stereogenys* had a cleft that separated palatines and maxillae on the midline. All three authors suggested that the cleft, open or not, was covered either by a membrane (Swinton, ibid.) or "broad, horny plates" (Andrews, ibid.), producing a secondary palate of the sort seen in mammals (and the cheloniids *Osteopygis, Erquellinesia,* and *Rhetechelys*). Despite the passage of years, it is still not clear whether the palate of the Stereogenyina had a functionally open slit down its midline or whether it was covered with something.

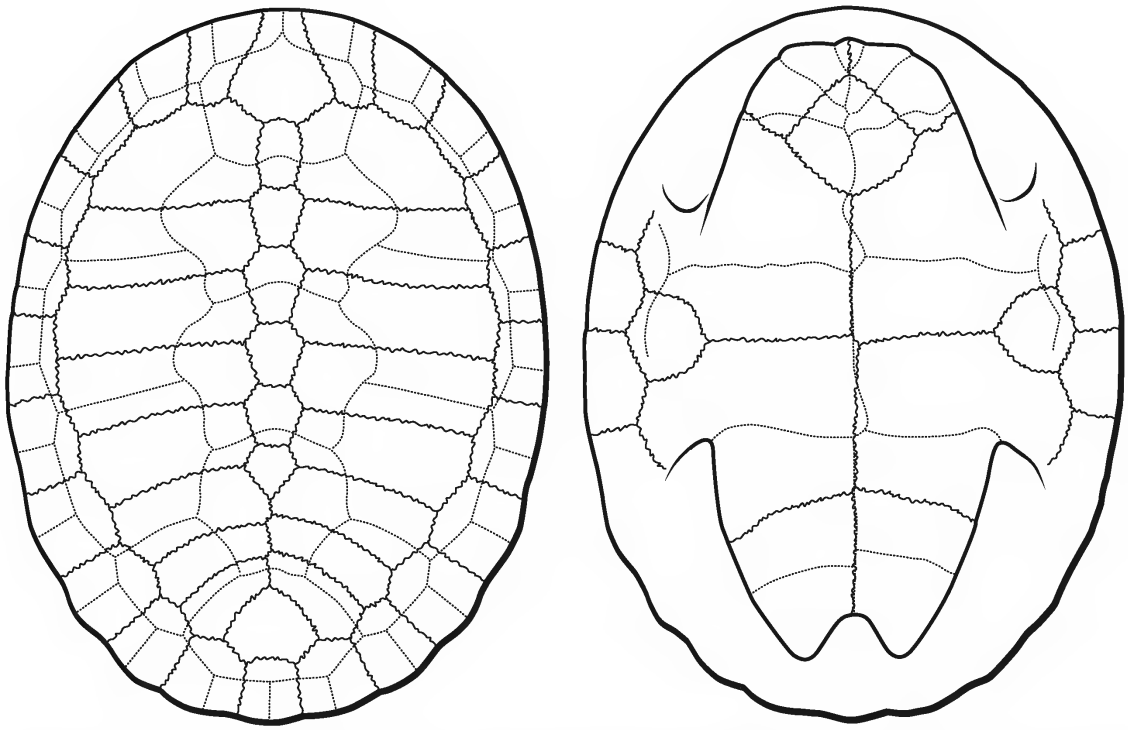

Fig. 87. *"Podocnemis" aegyptiaca* Andrews, 1900. Restored shell, based on Andrews (1900: pl. 1) and Fourteau (1920: fig. 21). [R. Wood, C. Wilson, del.]

The retention of the cleft in this group for a long time period over a fairly large area of marine landscape suggests that it was successful in doing whatever it did. Presumably, if the cleft was open in life, there could have been communication with the choanal passages, allowing some sort of air movement, either for breathing or sensing. Secondary palates have come and gone, evolutionarily speaking, but a complete secondary palate with a median fissure is something unique in tetrapods.

PALATINE

**Preservation:** In DPC 4120 the right palatine is complete; the left one lacks its anterolateral portion. BMNH R.3007 has the ventral and lateral surfaces of the palatine preserved on both sides, slightly crushed; only the anterior sutures are visible. AMNH 14736 has both palatines preserved but eroded. BMNH R.3189 has both palatines present; they are not well preserved and are crushed dorsomedially, coming in contact on the midline. This was the specimen that led Andrews (1901, ibid.; 1906: ibid.) to suggest that the palate in *Stereogenys* may have been completely closed. Both palatines of BMNH R.3190 are present but cracked and poorly preserved. BMNH R.3191 preserves the posteromedial parts of both palatines.

**Contacts:** The contacts in ventral view in *Stereogenys* are with the maxilla anterolaterally, the pterygoid posteriorly, and the basisphenoid posteromedially. The basisphenoid contact occurs only in *Stereogenys* and *Shweboemys* among the subtribe Stereogenyina, and is due to the unusually long basisphenoid. It completely separates the pterygoids on the midline. On the dorsal surface the palatine contacts the processus inferior parietalis. In the floor of the fossa orbitalis, i.e., the anterior surface of the septum orbitotemporale, the palatine contacts the maxilla anterolaterally, the jugal laterally, the postorbital posterolaterally, and the frontal dorsomedially. In the posterior surface of the septum orbitotemporale, the palatine contacts the jugal anteroventrally, the postorbital anterodorsally, the parietal

posterodorsally, and the pterygoid posteroventrally. The large dorsal process of the palatine that reaches the parietal and postorbital is found only in *Stereogenys* and *Shweboemys* among the subtribe Stereogenyina.

**Structures on dorsal surface:** In common with the other subtribe Stereogenyina members, *Stereogenys* has an unusually deep posterior pocket or concavity in the posterior wall of the fossa orbitalis (the septum orbitotemporale). The palatine forms the anterior part of the sulcus paltinopterygoideus.

The dorsal process of the palatine in *Stereogenys* is completely preserved and visible internally as well as externally. The process is particularly large and massive (possibly related to the extensive secondary palate, a major part of which directly underlies the process). The sulcus palatinopterygoideus, which is lateral to the palatine process is consequently reduced, particularly anteriorly where, instead of a large opening visible in anterior view (as in living pelomedusoides), it is reduced to a small opening far posterior to the postorbital wall itself. The sulcus palatinopterygoideus can be seen clearly in DPC 4120. When seen along its axis from a posteroventrolateral position, the sulcus palatinopterygoideus narrows significantly at its anterior end to become funnel shaped.

**Structures on ventral surface:** The palatine forms the lateral wall of the choanal passage or groove (fig. 82), and the long secondary palate, characteristic of the subtribe Stereogenyina. *Stereogenys* and *Shweboemys* have particularly long secondary palates, even among the subtribe Stereogenyina, and these are mostly formed by posterior extensions of the palatine. The medial edges of the palatine in *Stereogenys* and *Shweboemys* and *Lemurchelys* are parallel, rather than curved as in all the other subtribe Stereogenyina.

QUADRATE

**Preservation:** The right quadrate is present in DPC 4120 but lacks its anterior cheek plate, and there is some breakage along its posterolateral edge. BMNH R.3007 has the quadrate preserved on both sides; the right is crushed with no cavum tympani visible, the left has a cavum tympani. AMNH 14736 has both quadrates partially preserved but eroded. BMNH R.3189 has both quadrates missing, although on the left side the margin of the otic chamber lies on the canalis stapedio-temporale and some parts of quadrate may remain, but no sutures are visible. Most of the right quadrate in BMNH R.3190 is present showing the cavum tympani, but it is poorly preserved. Most or all of the left quadrate in BMNH R.3190 is missing. BMNH R.3191 preserves none of the quadrate.

**Contacts on lateral surface:** As preserved, none of the lateral surface contacts are preserved in *Stereogenys*, although the squamosal contact is presumed to be posterodorsal.

**Structures on lateral surface:** The cheek is not emarginated, although sutures are not visible in the specimens that show this. Only the posterior half of the cavum tympani is decently preserved in *Stereogenys* (in DPC 4120) and it shows a relatively deep cavum, similar to that in *Bairdemys*. The incisura columellae auris is completely enclosed along with the eustachian tube, as in the other subtribe Stereogenyina. The antrum postoticum in *Stereogenys* is very small, much as in *Lemurchelys, Bairdemys venezuelensis,* and *B. hartsteini*. The eustachian tube is not separated from the fenestra postotica in *Stereogenys* as it is in *Bairdemys*.

**Contacts on dorsal and anterior surface:** The quadrate in *Stereogenys* contacts the prootic anteromedially, the opisthotic posteromedially, presumably, the squamosal posteriorly and posterolaterally.

**Structures on dorsal and anterior surface:** The foramen stapedio-temporale is preserved in DPC 4120 and formed between the prootic and quadrate as in most turtles.

**Contacts on ventral surface:** On the ventral surface of DPC 4120 the contacts are with the pterygoid anteromedially and the basioccipital posteromedially. There is a very narrow contact with the basisphenoid that is virtually pinched out by the expanded pterygoid.

**Structures on ventral surface:** The quadrate forms the posterolateral part of the cavum pterygoidei, which appears to be about the same depth in *Stereogenys* as in *Lemurchelys* and *Bairdemys*, but not as deep as in

*Mogharemys*. The cavum pterygoidei in *Stereogenys* has the cavum cranii opening in its roof via the foramen cavernosum, formed by the pterygoid laterally and the quadrate medially.

**Contacts on posterior surface:** The quadrate of *Stereogenys* contacts the squamosal dorsolaterally, the opisthotic dorsomedially, and the basioccipital ventromedially.

**Structures on posterior surface:** The fenestra postotica in *Stereogenys* is not separated by bone from the sulcus eustachii as it is *Latentemys* and *Bairdemys*. The incisura columellae auris includes the eustachian tube as in the other subtribe Stereogenyina. The foramen chorda tympani inferius is not visible, but may be small and one of a number of small foramina in a damaged area.

PTERYGOID

**Preservation:** Both pterygoids are present in DPC 4120. The right one is complete except for the pterygoid flange and some breakage around the cavum pterygoidei. The left one is also nearly complete, but lacking the pterygoid flange and with some breakage posteriorly. BMNH R.3007 has the pterygoid preserved on both sides, slightly crushed, lacking sutures, with no internal surfaces visible. AMNH 14736 has both pterygoids preserved but eroded. BMNH R.3189 has portions of both pterygoids present, but they are not well preserved. The right one exposes the cavum pterygoidei; the left one retains the processus trochlearis pterygoidei. Parts of both pterygoids are present in BMNH R.3190 but poorly preserved with no sutures. The left pterygoid retains the processus trochlearis pterygoidei and both have some parts of the pterygoid flange base. BMNH R.3191 preserves the posteromedial parts of both pterygoids.

**Contacts on ventral surface:** The pterygoid in *Stereogenys* contacts the palatine anteriorly, the basisphenoid posteromedially, and the quadrate posterolaterally. Due to the anteriorly extensive basisphenoid, which reaches the palatines, the pterygoids do not meet on the midline. This also occurs in *Shweboemys* but not in any other subtribe Stereogenyina member.

**Structures on ventral surface:** The processus trochlearis pterygoidei in *Stereogenys* lies at a right angle to the midline as in the other subtribe Stereogenyina, and has a concavity on its ventral surface at the base. The cavum pterygoidei in *Stereogenys* has the cavum cranii opening in its roof via the foramen cavernosum, formed by the pterygoid laterally and the quadrate medially, as in *Latentemys*. The foramen nervi facialis is just anterior to the foramen cavernosum and is largely formed by the prootic. Probably some prootic enters the margin of the foramen cavernosum but this is unclear. The pterygoid forms the lateral rim of the anterior opening of the cavum pterygoidei into the cavum cranii.

The base of the pterygoid flange is preserved on many specimens of *Stereogenys*, but best seen in DPC 4120. It is a posterior extension of the medial limits of the concavity on the base of the processus trochlearis pterygoidei, parasagittal in position, and reaching the ventral opening of the cavum pterygoidei, as in other subtribe Stereogenyina that are well enough preserved to show these structures.

**Contacts on dorsal surface:** The posterior surface of the septum orbitotemporale shows these contacts with the pterygoid: the palatine anteroventrally and the parietal dorsally. The postorbital and jugal contacts seen in other subtribe Stereogenyina are prevented by the large dorsal process of the palatine in *Stereogenys* and *Shweboemys*. The crista pterygoidea contacts the palatine anteriorly and the parietal dorsally.

**Structures on dorsal surface:** The processus trochlearis pterygoidei in *Stereogenys* is similar to that in the other subtribe Stereogenyina. The floor of the sulcus palatinopterygoideus is formed anteriorly by the palatine and posteriorly by the pterygoid. It is more of an enclosed tunnel in the subtribe Stereogenyina than in other podocnemidids because of the thick septum orbitotemporale in this group. The foramen nervi trigemini is formed by the parietal anterodorsally, the prootic posterodorsally, and the pterygoid ventrally, as in other podocnemidids.

SUPRAOCCIPITAL

**Preservation:** Only the anteroventral part of the supraoccipital from the foramen magnum forward, remains in DPC 4120.

BMNH R.3007, BMNH R.3189, and AMNH 14736 have the anterior part of the supraoccipital preserved, but the crista supraoccipitalis is missing. BMNH R.3190 has the anterior portion as well as some of the crista supraoccipitalis. BMNH R.3191 preserves a small part of supraoccipital just anterior to the foramen magnum on the left side.

**Contacts and structures:** The supraoccipital contacts the parietal dorsally and anteriorly, the prootic anterolaterally, the opisthotic posterolaterally, and the exoccipital posteroventrally, as in other podocnemidids. The crista supraoccipitalis is missing in the available specimens, but AMNH 14735 (cast of the type) shows an indication of the horizontal shelf on the ventral edge of the crista in the subtribe Stereogenyina. The supraoccipital forms the dorsal edge of the foramen magnum. There is apparently no exposure of the supraoccipital on the skull roof in *Stereogenys*.

EXOCCIPITAL

**Preservation:** In DPC 4120 the right exoccipital is complete; the left one lacks its lateral process. BMNH R.3007, BMNH R.3189, and AMNH 14736 have the exoccipital area preserved on both sides, somewhat crushed, the condylus occipitalis is missing, and they lack sutures. BMNH R.3190 has both exoccipitals and part of the condylus occipitalis surface preserved. BMNH R.3191 preserves most of both exoccipitals.

**Contacts:** The exoccipital in *Stereogenys* contacts the supraoccipital dorsally, the opisthotic laterally, and the basioccipital ventrally.

**Structures:** As far as can be determined, the condylus occipitalis is formed equally by the basioccipital and the two exoccipitals. The foramen nervi hypoglossi are two openings medially that join in a recessed foramen to open posteriorly as one foramen, as in other members of the subtribe Stereogenyina. The foramen jugulare posterius is completely closed by bone, but in contrast to forms such as *Latentemys*, the exoccipitals do not meet to form the bar; the opisthotic is between the two lateral processes of the exoccipital and this closes the opening. Such variation is commonly seen in many recent turtles as well. The exoccipital does not enter the fenestra postotica.

BASIOCCIPITAL

**Preservation:** In DPC 4120 the basioccipital is complete except for the condylus occipitalis. BMNH R.3007, BMNH R.3189, and AMNH 14736 have the basioccipital area preserved, slightly crushed, and lacking sutures, with the condylus occipitalis missing. BMNH R.3190 has the basioccipital area with no sutures but with the condylus occipitalis preserved. The basioccipital is present but damaged in BMNH R.3191.

**Contacts and structures:** The basioccipital contacts the basisphenoid anteriorly, the quadrate laterally, the exoccipitals posterodorsally, and the opisthotic dorsolaterally. The basioccipital is relatively short in *Stereogenys* as in *Shweboemys* and in contrast to other subtribe Stereogenyina.

PROOTIC

**Preservation:** In DPC 4120 the right prootic is complete, and the left one lacks its lateral part. BMNH R.3007 and AMNH 14736 have the prootic area preserved on both sides, slightly crushed, with no sutures and no indication of the foramen stapediotemporale. In BMNH R.3189 the prootic is exposed on the left side showing the canalis stapedio-temporalis and the foramen stapedio-temporale. In BMNH R.3190 the prootic appears to be missing, badly damaged, or covered with plaster on both sides. The left prootic in BMNH R.3191 is present and nearly complete, but the right one is poorly preserved.

**Contacts:** The prootic in *Stereogenys* contacts the parietal dorsomedially, the quadrate laterally, the pterygoid ventrally, and the opisthotic posteriorly, as in other podocnemidids. Within the cavum pterygoidei the prootic also contacts the basisphenoid ventrally, the pterygoid laterally, and the quadrate medially.

**Structures:** The prootic in *Stereogenys* participates in the formation of the foramen nervi trigemini and the foramen stapediotemporale, which are formed by the same additional elements as in *Bairdemys* and *Latentemys*. Within the cavum pterygoidei the prootic forms the foramen nervi facialis in the roof of the cavum, and probably enters

the foramen cavernosum. Within the cavum cranii the prootic forms the fossa acusticofacialis, as in all turtles. The fossa acusticofacialis is unique in *Stereogenys* among turtles in being so far recessed that it appears to be a canal when seen from inside the cavum cranii. The two small foramina nervi acustici lie dorsally in the canal and the facial nerve is a larger canal extending ventrolaterally.

OPISTHOTIC

**Preservation:** In DPC 4120 the left opisthotic is missing, but the right one is complete. BMNH R.3007 and AMNH 14736 have the opisthotic area preserved on both sides, with no sutures. In BMNH R.3189 portions of both opisthotics are present, the left one is clearer, but sutures are lacking. BMNH R.3190 has most of both opisthotics, but the areas are poorly preserved. The medial portions of both opisthotics are present in BMNH R.3191.

**Contacts:** The opisthotic in *Stereogenys* contacts the supraoccipital anteromedially, the prootic anteriorly, the quadrate ventro- and anterolaterally, probably the squamosal posterolaterally, and the exoccipital posteromedially.

**Structures:** The opisthotic in *Stereogenys* enters the lateral margin of the foramen jugulare posterius and separates it from the fenestra postotica.

BASISPHENOID

**Preservation:** In DPC 4120 the basisphenoid is complete and visible internally as well as externally. BMNH R.3007 and AMNH 14736 and BMNH R.3189 have the basisphenoid area preserved, but no sutures are visible. The area of the basisphenoid in BMNH R.3190 is preserved, but there are no sutures. The basisphenoid is preserved in BMNH R.3191.

**Contacts on ventral surface:** The basisphenoid in *Stereogenys* contacts the palatines anteriorly, the pterygoids laterally, the basioccipital posteriorly, and the quadrate posterolaterally in a very narrow suture.

**Structures on ventral surface:** The large basisphenoid of *Stereogenys* and *Shweboemys* roofs much of the posterior part of the skull and forms the roof of the posteriorly displaced apertura narium interna. The basisphenoid forms the medial and anteroventral walls of the cavum pterygoidei, and the foramen posterius canalis carotici interni.

**Contacts on dorsal surface:** The basisphenoid contacts the pterygoid anterolaterally, the prootic laterally, the exoccipital posterolaterally, and the basioccipital posteriorly.

**Structures on dorsal surface:** The rostrum basisphenoidale in DPC 4120 is unclear as the anterior edge of the basisphenoid here is broken. The sulcus cavernosus extends from the anterior opening of the cavum pterygoidei forward, as in other subtribe Stereogenyina members. The dorsum sellae is unusual in being almost completely flat, with no clear step separating it from the sella turcica. Just medial to the anterior opening of the cavum pterygoidei lies the foramen anterius canalis carotici interni, connected by a short canalis caroticus internus to the foramen posterius canalis carotici interni, which is in the cavum pterygoidei. Between the anterior opening of the cavum pterygoidei and the foramen anterius canalis carotici interni is a short processus clinoideus. A foramen nervi abducentis was not seen but could be present.

The dorsal surface of the basisphenoid is visible and well preserved in *Stereogenys* (DPC 4120) and *Latentemys* (BMNH R.11998). In both the anteriormost limits are missing and in DPC 4120 there may be some erosion of bone surfaces. In *Latentemys* the rostrum basisphenoidale is fused in front of the sella turcica to form a rodlike projection. In *Stereogenys* there is no fusion and the trabeculae are very short, barely extending past the foramen anterior canalis carotici interni. The sella turcica in *Latentemys* is a distinctly formed, oval concavity, similar to *Podocnemis*, but in *Stereogenys* the sella turcica appears to be very shallow. The dorsum sellae is relatively high and overhanging slightly in *Latentemys*, but in *Stereogenys* it is low and flat, with no midline indentation or concavity at the level of the foramen anterior canalis carotici interni. These paired foramina are relatively close together and hidden in dorsal view in *Latentemys*. In *Stereogenys* the foramina canalis carotici interni are visible dorsally and wider apart than in *Latentemys*. In both specimens the paired processus clinoideus is broken off on

each side, but the processus base is preserved and seems to be much smaller in *Stereogenys*. Unfortunately, there is insufficient material of other taxa to make useful systematic use of these features at present.

The cavum pterygoidei is broken open on the left side of DPC 4120 revealing its internal morphology. Basically its structure in *Stereogenys* is comparable to that in *Podocnemis* with the important exception of the lateral head vein. In *Podocnemis* the lateral head vein is separated by bone from the cavum pterygoidei, and there is a well-defined canalis cavernosus. In *Stereogenys* (and *Latentemys, Erymnochelys,* and *Peltocephalus*) the lateral head vein enters the cavum pterygoidei in the dorsal roof of the latter just posterior to the foramen for VII and immediately ventral to the aditus stapedio temporalis.

Both the facial nerve and the lateral head vein exit the aditus together in a short canal that should be the canalis cavernosus. This canal, however, is very different in length to the more normal canalis cavernosus seen in *Podocnemis*. This condition of the lateral head vein entering the cavum pterygoidei also occurs in *Latentemys, Erymnochelys,* and *Peltocephalus* (see discussion in character list). The facial nerve and the lateral head vein enter the cavum pterygoidei by means of a joint depression in the roof of the chamber. On the left side of DPC 4120 the break goes through the middle of this depression, between facial nerve and lateral head vein, so that the entry foramen of both is missing. The facial nerve shortly exits (actually it's entering) while the lateral head vein goes anteromedially to enter the cavum cranii at the extreme anterior end of the cavum pterygoidei.

The bones making up the cavum pterygoidei in *Stereogenys* are complex but comparable to *Podocnemis* despite the absence of the lateral head vein in the chamber of *Podocnemis*. The floor is formed by the pterygoid, which has ridges that attach to the more dorsal elements on each side. Laterally the quadrate contacts the pterygoid posteriorly, and the prootic contacts it more anteriorly. This suture rises anteriorly to reach the roof of the chamber anteromedially, and it enters the edge of the foramen for the entry of the facial nerve and lateral head vein.

On the medial wall of the cavum pterygoidei, the pterygoid is lower and contacts the quadrate posteriorly and the basisphenoid anteriorly. The foramen posterius canalis carotici interni is formed by the basisphenoid ventrally and the prootic at least anterodorsally. The bone making up the posterior rim is not clearly identifiable but seems to be basisphenoid. The prootic-basisphenoid suture is unclear. The anterior opening of the cavum pterygoidei is formed by pterygoid ventrally, basisphenoid ventromedially, and prootic dorsally.

## SHELL MORPHOLOGY OF SOUTH AMERICAN LATE CRETACEOUS AND EARLY TERTIARY PODOCNEMIDIDS

Figures 88–97; table 4

The six extinct taxa described here (see Systematics above for more information on each species) are *Bauruemys elegans* (Suarez, 1969a, 1969b), Peirópolis A, Peirópolis B, *Cambaremys langertoni, Roxochelys wanderleyi*, and *Lapparentemys vilavilensis*. We again need to emphasize that the individually disarticulated bones that we identify as Peirópolis A and Peirópolis B are, with a few stated exceptions, not associated with other elements. We informally associate them on the basis of size, differences from *Cambaremys*, and in the case of some Peirópolis A material, with autapomorphic morphology of three articulated and/or associated shells. It is even possible that there are more than three species in these collections, although we have seen no evidence for this. Our speculative association of the smaller Peirópolis B shell elements with the smaller skull of *Peiropemys* and the larger Peirópolis A shell elements with the larger skull of *Pricemys*, is based only on size, and that is why we have not formalized or used these associations in the phylogenetic analysis.

(1) *Bauruemys elegans* is described on the basis of the type description in Suarez (1969b), Kischlat (1994), restudy of the type specimen, MCT 1492-R, and 18 other specimens available to us. These consist of 11 uncataloged specimens in the DNPM (here designated 1969-1 through 1969-11),

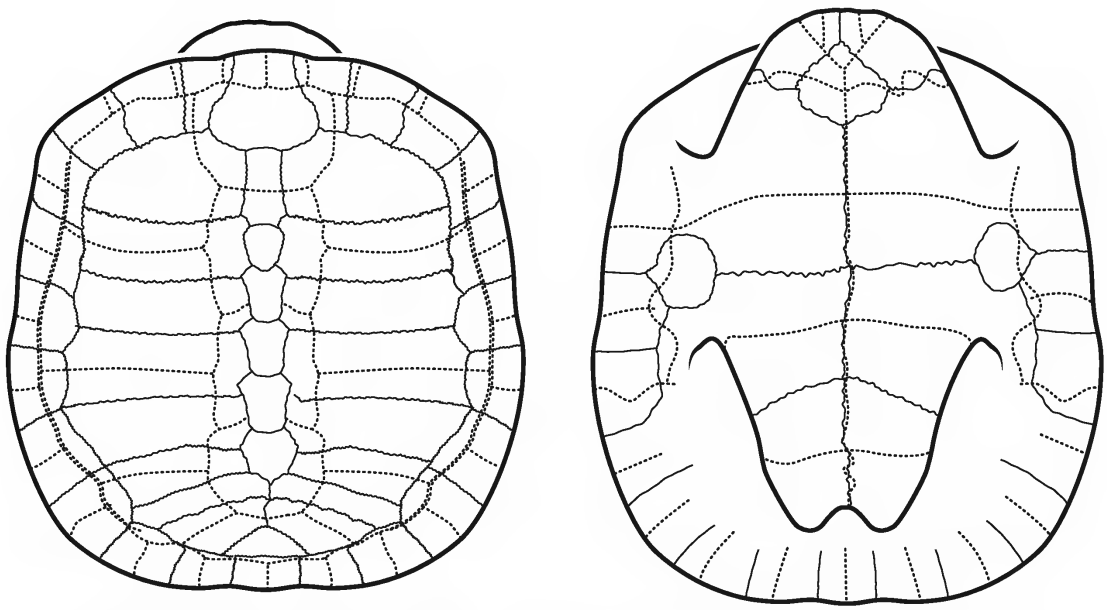

Fig. 88. *Bauruemys elegans* (Suárez, 1969a). Partially restored shell. [F. Ippolito, del.]

MCZ 4122, MCZ 4125, MN 4327-V, MN 4348-V, MN 4349-V, MN 4487-V, and MN uncataloged.

(2) Peirópolis A is represented by a large number of disarticulated shell bones from the Caiera Quarry near Peirópolis (see Locality discussion under *Peiropemys mezzalirai,* n. gen, et sp., for more information), mostly complete single bones but not associated or articulated with other bones. Included with these are three partly or fully articulated specimens:

(a) DGM Peirópolis 321, a complete plastron with at least some carapace and some cervical parts, all disarticulated. The plastron of 321 is in a drawer labeled: "Desmonte 1967 Peirópolis Mun. Uberaba."

(b) MCT 1499-R, a large shell from Caiera Quarry (shown on Price's map in the 1953 excavation area, reproduced in Kellner et al., 2005: fig. 3). Most of the carapace, the plastron, pelvis, and first thoracic are present. It is prepared with the plastron side up; some of anterior lobe is separate.

(c) Another Peirópolis shell, possibly not from Caiera Quarry, and collected by Langerton, has a thickened dorsal lip of the epiplastra, which appears to be characteristic of Peirópolis A.

(3) Peirópolis B is the smallest of the three shell taxa from this area and the one for which there is the most limited amount of material. The material is all disarticulated, but some of it is associated. At present we have the nuchal, costals 1, 5, 7 and 8, peripherals 1, 8–11, the suprapygal and pygal. We cannot assign any plastron material to this taxon with certainty at this time, although we speculate that some of the small plastral elements may belong to this species.

(4) *Cambaremys langertoni* França and Langer, 2005, is also from the Peirópolis quarries site, but not the same actual excavations made by the DNPM in 1949, 1950, 1953, 1955, 1957, 1958, 1959, and 1961. This specimen differs from both Peirópolis A and Peirópolis B (table 4, discussion above). Thus we include *Cambaremys langertoni* as a separate taxon based on França and Langer (2005), as well as the dissertation in which the type, and only known specimen (CPP-0252), is described in detail (França, 2004), and a subsequent publication on the type (França and Langer, 2006). Romano et al. (2009) consider it a synonym of *Roxochelys wanderleyi*; however, we disagree with this assignment (see discussion under *Cambaremys* in Systematics above).

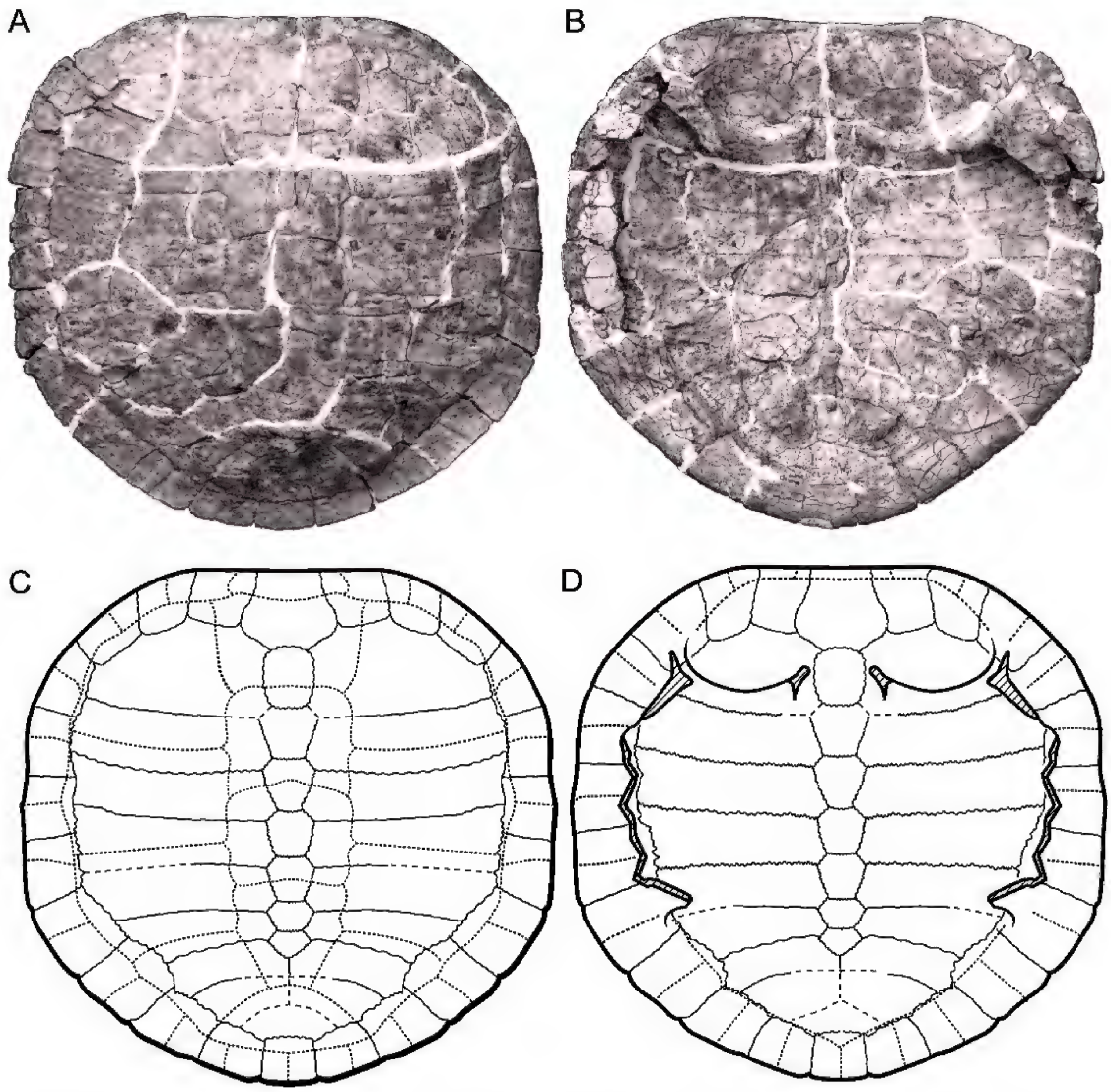


Fig. 89. *Lapparentemys vilavilensis* (Broin, 1971), n. gen. Shell. RM 20.5155. [F. Ippolito, del.]

(5) *Roxochelys wanderleyi* is based on the type specimen, DGM 216, and two other more complete shells. We follow Romano et al. (2009: figs. 2B, 3C) in identifying a complete shell, DGM uncataloged, collected by S. Mezzalira, as belonging to *Roxochelys wanderleyi*. We also identify MCT 1722-R [= DNPM LE307], collected by J. Martin Suárez as this species. Each consists of a complete carapace and plastron prepared inside and outside. Both the DGM uncataloged (Mezzalira specimen) and MCT 1722-R can be referred to *Roxochelys wanderleyi* based on highly extensive buttresses with thickened second costal, surface ornament similar to type, and similar scalation of the anterior plastral lobe (table 4).

(6) *Lapparentemys vilavilensis* consists of the type material, as well as other material referred to this taxon by Broin (1991), including MHNC 6903, MHNC 6904, MNHNP VIL-3 and MNHNP VIL-6; as well as WUS 2160, a nearly complete shell with skull; AMNH 14444, the central portion of a shell associated with a complete skull; and RM 20.5155, a complete but fragmen-

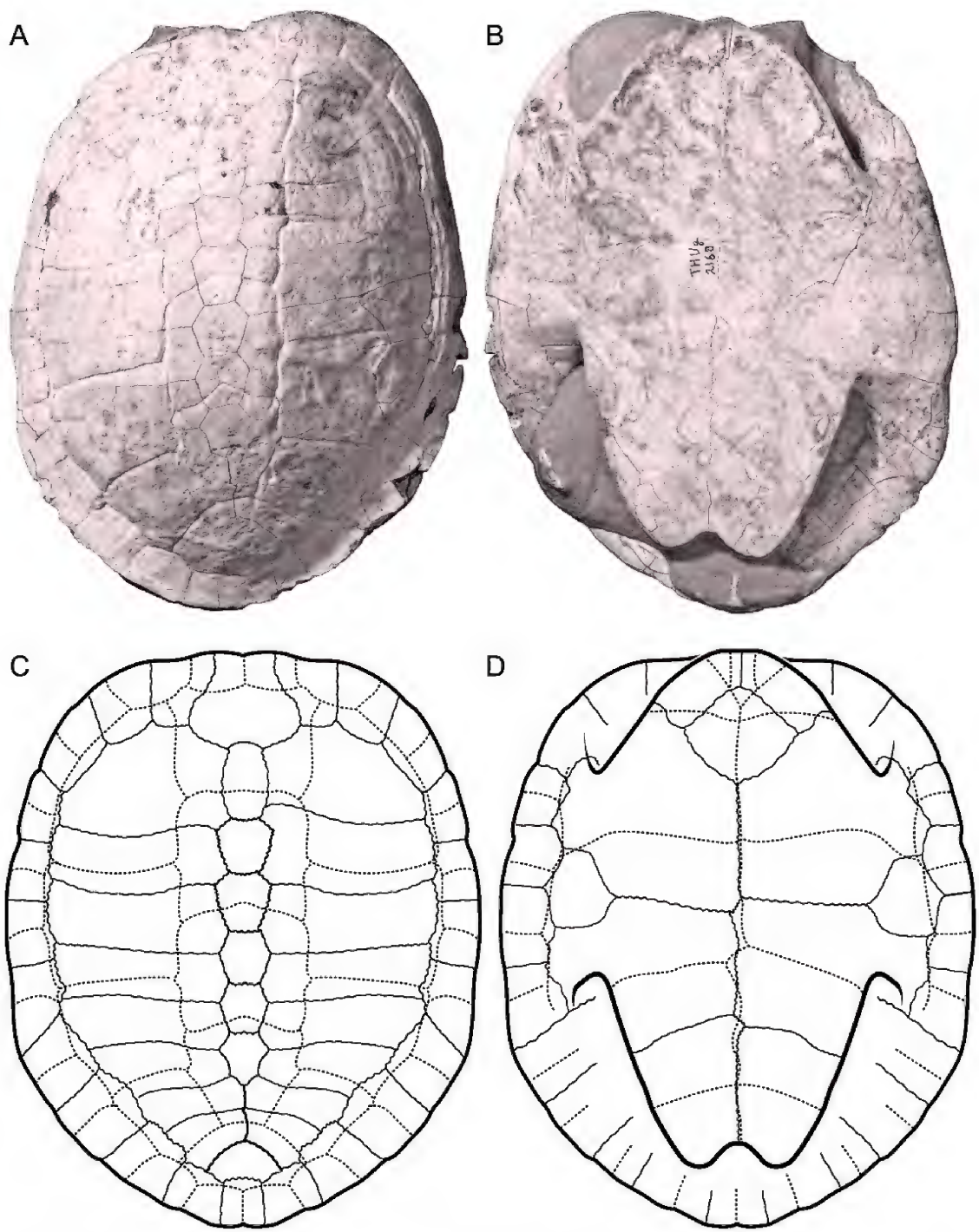


Fig. 90. *Lapparentemys vilavilensis* (Broin, 1971), n. gen. Shell. WUS 2160. [F. Ippolito, del.]

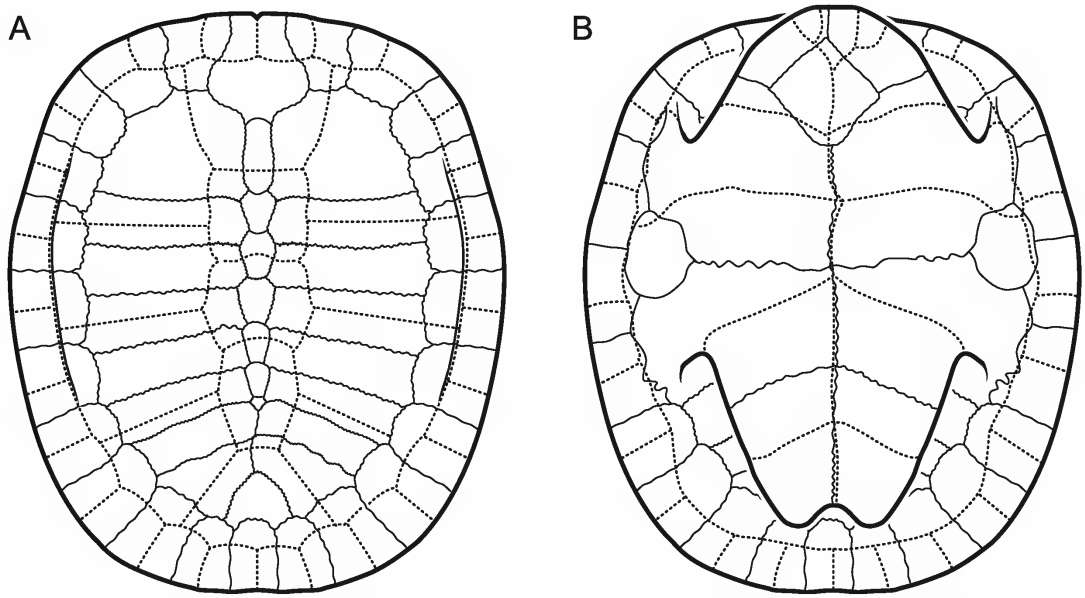


Fig. 91. Shell attributed to unnamed taxon Peirópolis A. **A,** Carapace speculatively restored from disarticulated parts (see text); **B,** plastron, DGM MCT 1499-R, a complete shell, with unprepared carapace. [F. Ippolito, del.]

tary shell associated with a poorly preserved skull. Some of the material referred to this taxon by Broin (1991), MHNC 6904 and MNHNP VIL-6, we believe actually represent two additional unnamed taxa and were not used in our concept of *Lapparentemys vilavilensis*. This question is discussed further under *Lapparentemys vilavilensis* in Systematics.

### Bones of Carapace in External View

**Surface ornamentation:** The surface of the shell of podocnemidids is not usually sculptured or strongly textured, however, there are exceptions. Well-preserved shells of *Bauruemys elegans* show distinctive parallel ridges around the edges of scales of the carapace along with ridges that radiate out from growth centers. The parallel ridges are concentric with respect to the growth centers of the shell and vary in width in MCZ 4125 and are thus remarkably similar to growth rings like those seen in the emydid *Malaclemys*. Interpretation of these concentric lines as growth rings would be consistent with the paleoecology of this species. The large number of fossils at the Presidente Prudente site could possibly be the result of a mass die-off that might be consistent with a seasonal environment. Such a seasonal environment could possibly produce growth rings. In the type shell of *Bauruemys elegans*, MCT 1492-R, radiating lines are weakly developed and concentric growth rings are visible only on the plastron. In other specimens, including MCZ 4125 and DNPM uncataloged 1969 #3, growth rings are clearly visible. In others (DNPM uncataloged 1969 #6) they are entirely absent. Growth rings and regular radiating ridges are present in many turtles from *Chelus* to *Chelydra* and are not likely to be systematically useful.

A very different pattern of ornamentation is present in the type of *Roxochelys wanderleyi*, MCT 1722-R. Broin (1991: 512) describes this ornamentation as "a reticulation of the surface in small polygones (sic) or dichotomous sulci." A similar ornamentation is present in some chelids such as *Hydromedusa* and *Phrynops* and also the bothremydid, *Taphrosphys*. Among the specimens studied, this fine anastomosing pattern of ornamentation of the bone surface is also seen in MCT 1722-R, and MCT Mezzalira shell (see also Broin, 1991: 512). Within the group under study here we consider this pattern to

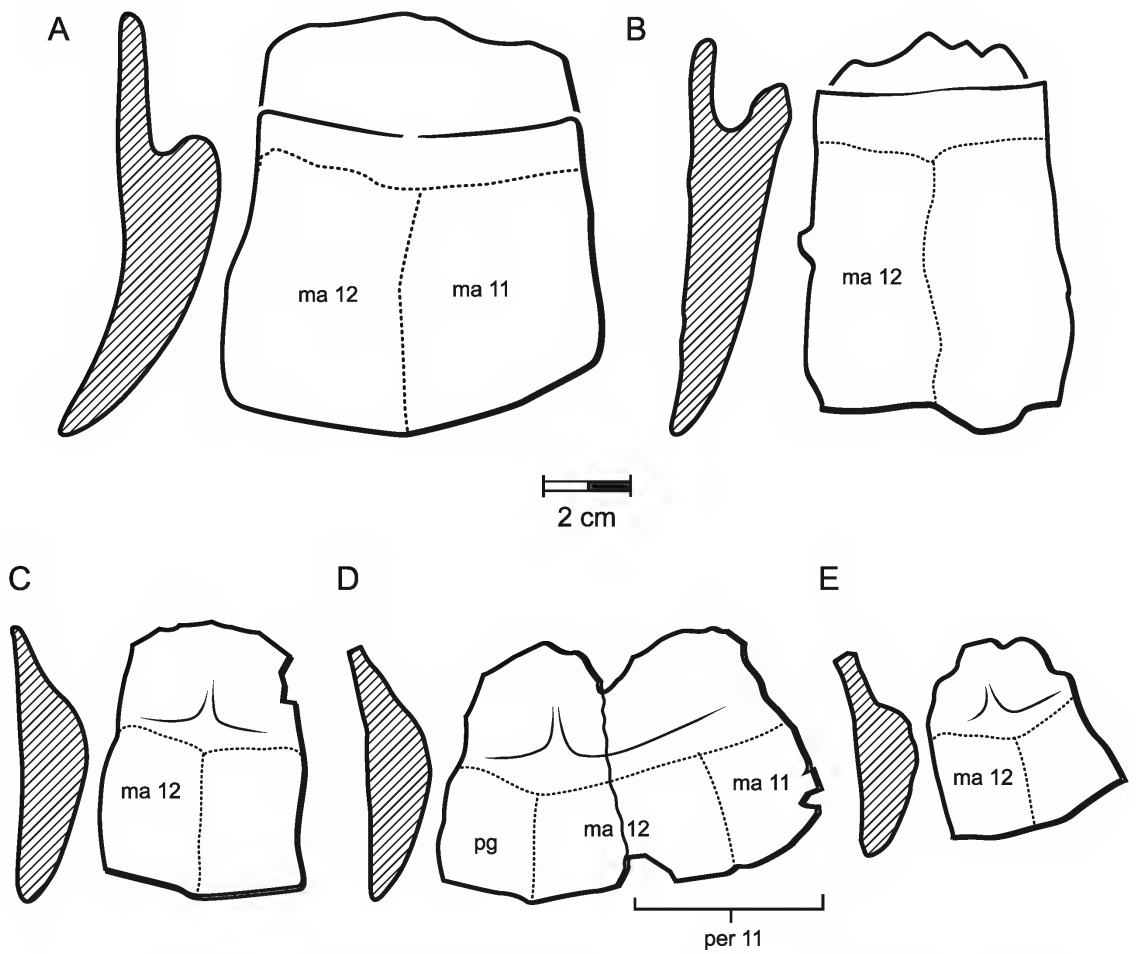


Fig. 92. Pygal and adjacent peripheral bones attributed to unnamed taxa Peirópolis A (upper row) and Peirópolis B (lower row) in ventral view, side views on left. All are DNPM DGM uncataloged (see text entries) from Caiera Quarry, near Uberaba, Minas Gerais State, Brazil. Serra da Galga Member, Marília Fm., Maastrichtian. See text entries for Peirópolis A and Peirópolis B (also *Peiropemys mezzalirai,* n. gen. et sp.) for further information. **A,** Peirópolis A pygal; **B,** Peirópolis A peripheral 11; **C,** Peirópolis B pygal; **D,** Peirópolis B pygal with articulated left peripheral 11 attached **E,** Peirópolis B pygal. [F. Ippolito, del.]

be an autapomorphy for *Roxochelys*. As an autapomorphy, it does not appear in the data set, but its absence from shells of *Lapparentemys* supports our assertion that this form is not allied to *Roxochelys*. Hutchison and Weems (1998) have argued that the similar network of fine grooves on the scaled surfaces of *Taphrosphys* shells may possibly have a vascular function. The same could be true of the ornamentation present on the scaled surfaces of *Roxochelys*, especially on the plastron.

There is variation in shell surface texture among the Peirópolis shell forms. Peirópolis A has a weak pattern of striations visible only in very well-preserved material possibly referred to this species, such as the complete nuchal associated with first costal and first and second peripherals. The smallest form from Peirópolis, Peirópolis B, has weak parallel ridges of the kind seen in *Bauruemys*, only less developed. *Cambaremys* has no distinctive ornamentation on the external surface of the shell (França and Langer, 2005). Broin (1971) describes that ornamentation of *Lapparentemys* as variable, but it is never very well developed and not comparable to that of *Bauruemys* or *Roxochelys*

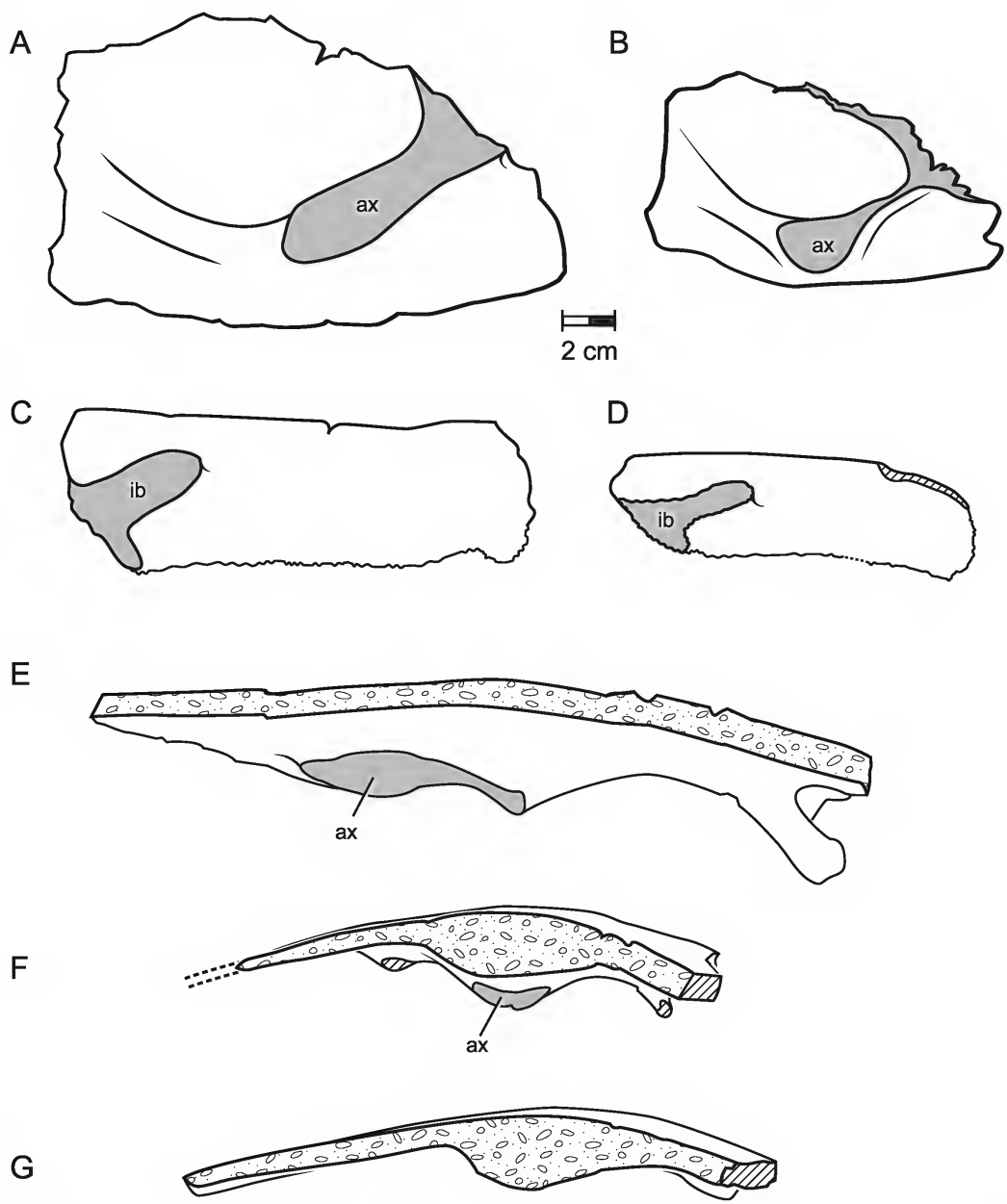


Fig. 93. Costal bones attributed to unnamed taxa Peirópolis A and Peirópolis B (see text entries for these taxa), showing axillary and inguinal buttress attachment sites. All are DNPM DGM uncataloged from Caiera Quarry, near Uberaba, Minas Gerais State, Brazil. Serra da Galga Member, Marília Fm., Maastrichtian. See text entries for Peirópolis A and Peirópolis B (also *Peiropemys mezzalirai,* n. gen. et sp.) for further information. **A,** first left costal in ventral view, Peirópolis A; **B,** first left costal in ventral view, Peirópolis B; **C,** fifth right costal in ventral view, Peirópolis A; **D,** fifth right costal in ventral view, Peirópolis B; **E,** Peirópolis A, first left costal in posterior view, midline to right; **F,** Peirópolis B, first left costal inposterior view, midline to right; **G,** Peirópolis B, second right costal in anterior view to show swelling of costals one and two contact behind axillary buttress. [F. Ippolito, del.]

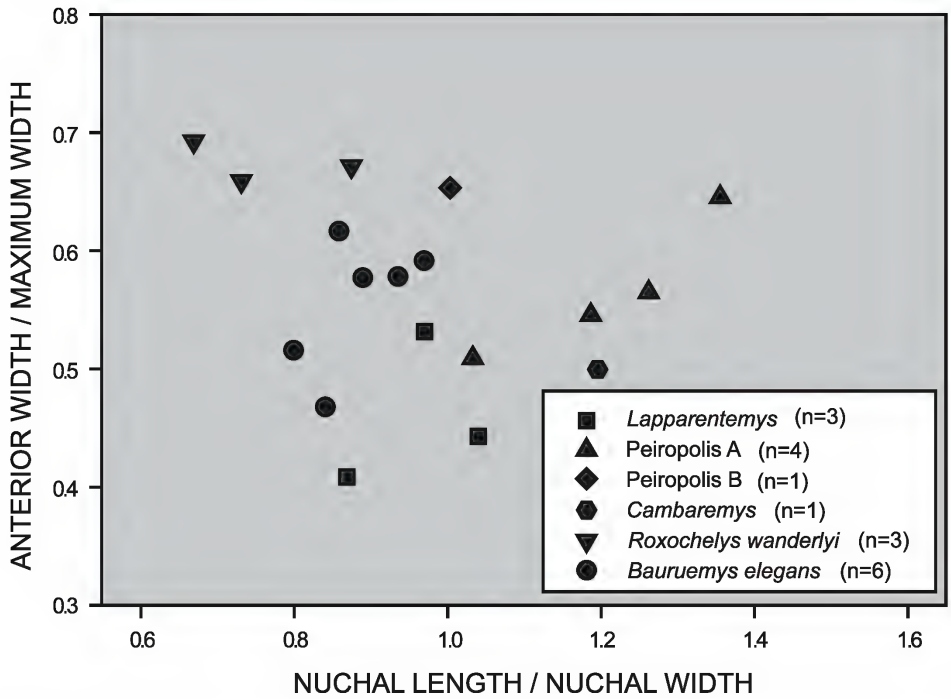


Fig. 94. Plot of nuchal shape in some South American Cretaceous and Early Tertiary podocnemidids. [P. Meylan, F. Ippolito, del.]

*wanderleyi*. The surface of the shell of *Podocnemis* is typically rather smooth.

**Nuchal contacts and shape:** The nuchal bone in *Bauruemys elegans,* as in nearly all podocnemidids, contacts the first peripheral anterolaterally, the first costal posterolaterally, and the first neural posteromedially. The only exception to these contacts occurs in

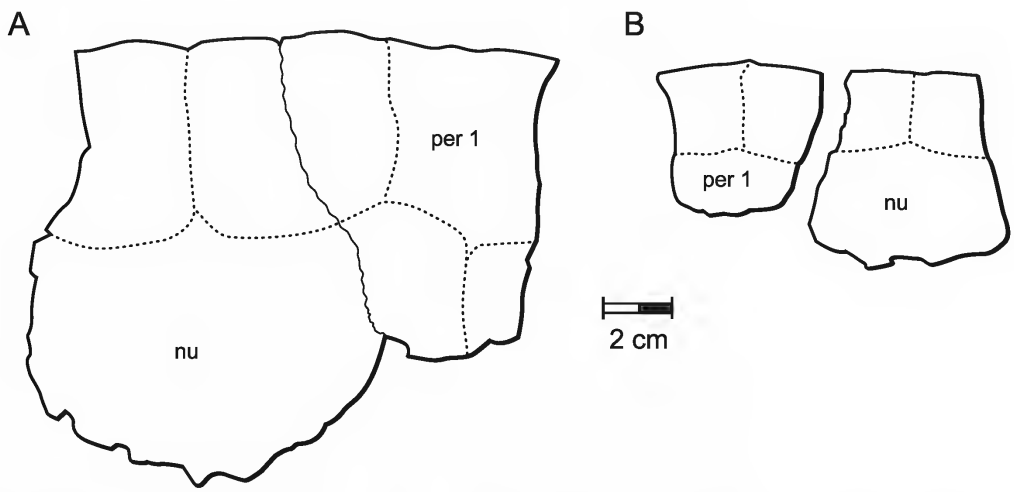


Fig. 95. Nuchals attributed to unnamed taxa, Peirópolis A and Peirópolis B (see text entries for further discussion). All are DNPM DGM uncataloged from Caiera Quarry, near Uberaba, Minas Gerais State, Brazil. Serra da Galga Member, Marília Fm., Maastrichtian. **A,** nuchal and first right peripheral of Peirópolis A; **B,** nuchal and first left peripheral of Peirópolis B. [F. Ippolito, del.]

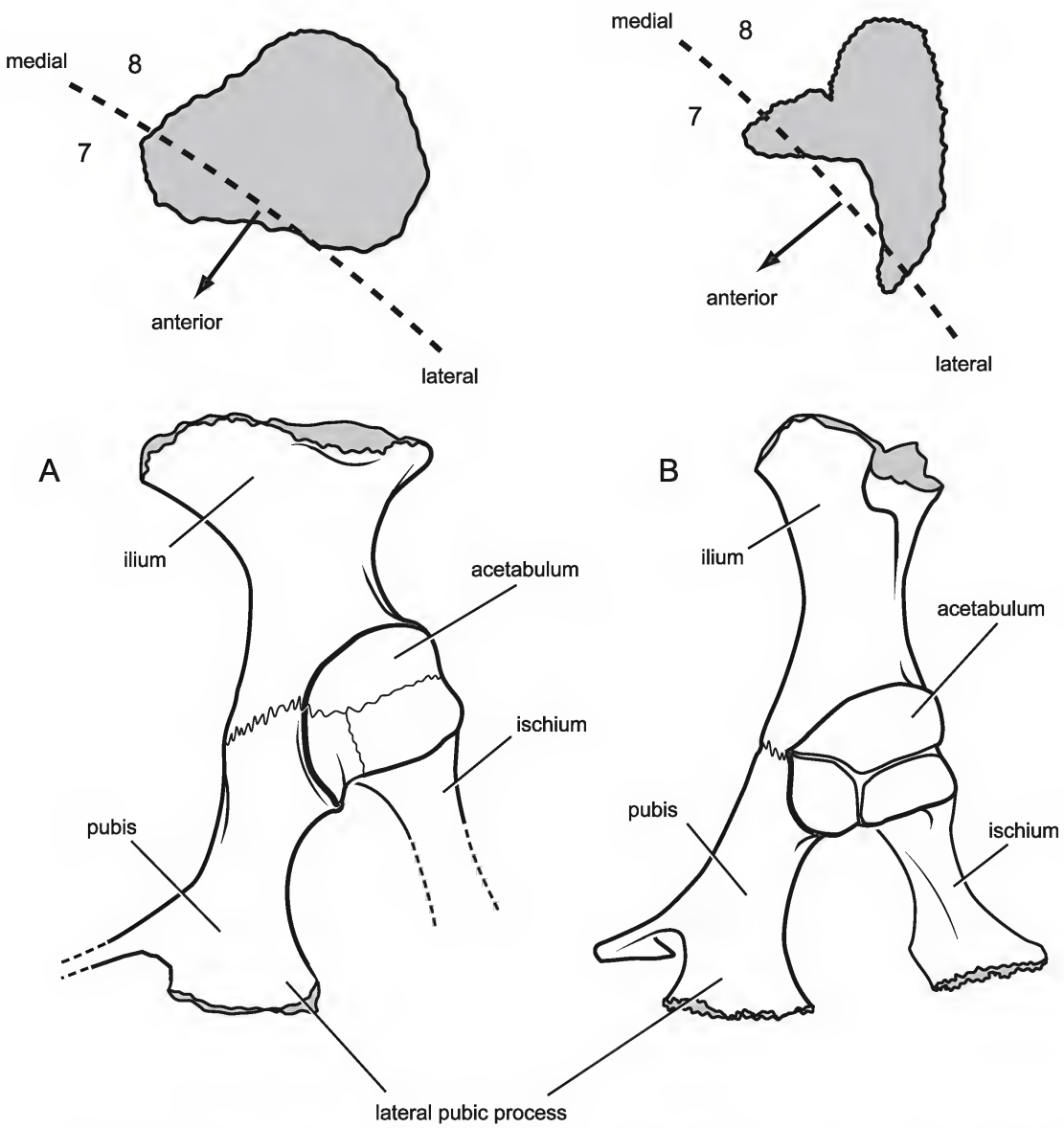


Fig. 96. Pelves and iliac attachment sites of podocnemidids, left pelvis in lateral view with iliac sutural area indicated above showing position of costals seven and eight. **A,** Peirópolis A, DNPM DGM uncataloged from Caiera Quarry, 1974, near Uberaba, Minas Gerais State, Brazil. Serra da Galga Member, Marília Fm., Maastrichtian. **B,** *Podocnemis expansa* AMNH 62947, Recent. [F. Ippolito, del.]

those forms in which the first costals meet on the midline between the nuchal and first neural. The nuchal bone in *Bauruemys* is slightly wider than long in all specimens available to us (fig. 94). It is about 15% of carapace length. It narrows anteriorly more than in *Roxochelys* but less than in *Lapparentemys*. The widest point occurs three-quarters of the way along its length so the nuchal appears more hexagonal in *Bauruemys* than in species in which this point is more posterior (*Cambaremys, Portezueloemys*, *Podocnemis*). The nuchal in *Roxochelys* is also wider than long (fig. 94) and does not narrow markedly along the anterior margin. The anterior margin is the widest among the

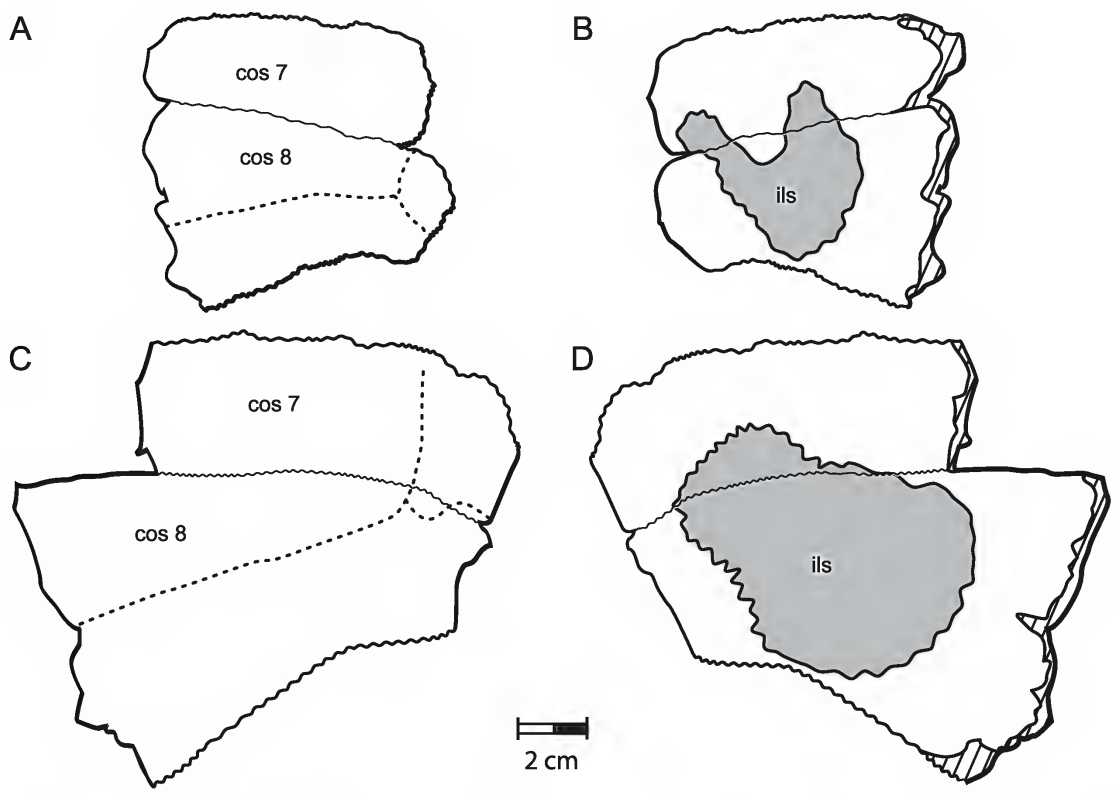


Fig. 97. Comparison of left costals seven and eight attributed to unnamed taxa Peirópolis A and Peirópolis B (see text entries for these taxa). All are DNPM DGM uncataloged from Caiera Quarry, near Uberaba, Minas Gerais State, Brazil. Serra da Galga Member, Marília Fm., Maastrichtian. Anterior toward top of page. **A, C,** dorsal views, medial to right; **B, D,** ventral views, medial to left. **A** and **B** are hypothesized as Peirópolis B; **C** and **D** are hypothesized as Peirópolis A. [F. Ippolito, del.]

taxa of interest, about 67% of maximum nuchal width. In *Lapparentemys* the anterior margin of the nuchal bone is very narrow and the anterolateral sides converge more noticeably. The anterior margin is about 42% of maximum nuchal width.

In all of the South American taxa included here, as in all known pelomedusoides, the cervical scale is absent. The first pleural scales do not reach the nuchal so this element is covered by the first vertebral scale posteriorly and the paired first marginal scales anteriorly. The first pleural contact with the nuchal appears to be absent among podocnemidids. Among bothremydids, it is absent from all known nuchal bones except for those of two genera within the Bothremydini, *Chedighaii* and *Araiochleys* (Gaffney et al., 2006).

Much of the variation in the shape of the nuchal bone reflects differences in the relative lengths of the contact of the first costal and first peripheral. In some forms the contacts of the first costal are shorter, and the suture is more transverse (most *Podocnemis*), and the overall nuchal shape is more trapezoidal. In others this contact is longer and at a lower angle relative to the midline making the nuchal more hexagonal (*Bauruemys*). Forms with longer nuchal bones generally have longer contacts between the nuchal and first peripherals. Variation in nuchal shape is not well suited to treatment as a discretely variable character; however, figure 94 suggests that four of the taxa of interest have nuchals that are nearly always wider than long and two have nuchals that are nearly always longer than wide.

There are two distinct nuchal morphologies among the unnamed material from Peirópolis. The more common one, presumed

to be Peirópolis A, is a longer nuchal with the widest point more posterior, as in *Cambaremys* and *Podocnemis*. The other, treated here as Peirópolis B, is shorter and wider anteriorly, more similar to *Bauruemys elegans* and *Roxochelys*. In Peirópolis A, the nuchal—first peripheral suture is markedly sinuous in the specimen used in the reconstruction (figs. 91, 95). This suture is straight in *Cambaremys*. In Peirópolis A there is also a slight midline notch and the anterior margin is slightly scalloped. In Peirópolis B, as in *Bauruemys elegans* and *Lapparentemys*, the anterior margin is straight.

**Neural series:** The neural series in *Bauruemys* is typically made up of six elements (fig. 88). In most specimens we have seen, the second neural is four sided and the seventh and eighth costals meet on the midline between the last neural and a single suprapygal. In all six of the South American podocnemidids in this study the neural series contacts the nuchal anteriorly. Contact of the neural series to the suprapygal does not occur in podocnemidids, but some have longer neural series than that seen in typical *Bauruemys*. One of seven complete neural series in *Bauruemys* includes a small seventh neural that partially separates the seventh costals (MN 7017-V; Romano, 2008), but it is asymmetrical and appears to be anomalous. In *Roxochelys wanderleyi* there is a seventh neural present in one specimen (MCT 1722-R) but six in the other (Mezzalira, DGM uncataloged, figured in Romano et al., 2009: figs. 2B, 3C); the carapace of the type specimen is incomplete. Similarly in *Lapparentemys,* some have six neurals (WUS 2160) and some have seven (RM 20.5155, MHNC 6904, MNHNP VIL 1). *Cambaremys* has been reconstructed with seven neurals and Peirópolis A with six. Reconstruction of the former seems certain; the latter is more tentative. Too much of the carapace of Peirópolis A remains unknown to reconstruct the neural series with certainty.

*Bauruemys* appears to be the only taxon in this study in which all specimens have a four-sided second neural. In other taxa a four-sided first neural is the dominant condition. However, among the three neural series that we consider to represent Peirópolis A, the four-sided neural is number one in two and number two in the other. In *Lapparentemys* the four-sided first neural is present in the type and RM 20.5155, but in WUS 2160 the contact between the first and second neurals is asymmetrical with the first neural in contact with the second right costal. Thus, among the taxa of interest here, the neurals offer no concrete characters that help to determine relationships.

The neural series is complete to the suprapygal and excludes midline contact of posterior costals in *Platychelys, Euraxemys, Cearachelys*, some species of *Pelusios* and some specimens of *Araripemys barretoi*. The degree of variability of this character within certain genera makes it of questionable phylogenetic value.

**Peripherals:** There is variation in the degree of guttering at the pleuro-marginal sulcus on the bridge peripheral bones. Distinct guttering is present along the bridge in *B. elegans*. Among the disarticulated material from Peirópolis there are bridge peripherals of two distinct types; some are guttered like those of *B. elegans*, but others are completely smooth and without gutters. Guttering of the bridge peripherals is present on peripherals six and seven on the left bridge of the large white shell that is the best specimen of Peirópolis A. Thus, we consider the bridge peripherals of Peirópolis A to be guttered, those of Peirópolis B to be unguttered. In *Cambaremys*, the pleuro-marginal sulcus is described as being superimposed on the costo-peripheral sutures (França and Langer, 2005), which would suggest that guttering is absent. Shallow guttering is also present in the bridge peripherals of *Lapparentemys* in WUS 2160 to the extent seen in *B. elegans* (specimen 1969-3). In *Lapparentemys* these costo-marginal sulci are clear but not as deeply incised as the lateral sulci of the vertebral scales. Bridge peripherals were not preserved with the type of *R. wanderleyi*, but in the two referred specimens, guttering is absent on the bridge peripherals.

Variation is present in the peripheral contacts with the bridge peripherals. In *B. elegans*, contact of the third peripheral with the axillary buttress is clear in the type and 1969-1. Contact of the eighth peripheral to the inguinal buttress is clear in 1969-4, showing that peripherals 3–8 contribute to

the bridge. These contacts can also be seen in two specimens of *Lapparentemys* and one complete and one reconstructed specimen of "Peirópolis 321," as well as the Mezzalira specimen of *R. wanderleyi*. *Cambaremys* differs from these forms in having the axillary buttress in contact with peripheral 2 (França and Langer, 2005).

Peirópolis A appears to possess an uncommon set of contacts of the posterior peripherals. At least one point of evidence that the reconstructed carapace and good plastron specimen are both referable to Peirópolis A comes from an unusual arrangement of the posterior peripherals and costals. In most podocnemidids each posterior peripherals contacts two adjacent costals. In both specimens of Peirópolis A, costal 8 is very wide and contacts peripherals 9, 10, and 11 (fig. 91). Costal 7 is correspondingly narrow, so peripheral 9 contacts costals 6, 7, and 8. This is clear in the associated set of posterior elements used in the reconstruction of Peirópolis A and also on the interior surface of the carapace of the specimen with the complete plastron, DGM MCT 1499-R (fig. 91). The same arrangement has also been observed in the three specimens of *Podocnemis*, the extinct "*P.*" *negrii* (Caravalho et al., 2002) and in two recent species *P. expansa* (PCHP 4711) and *P. unifilis* (P.A.M. unnumbered).

**Pygal region:** Most Pelomedusoides have a single suprapygal, which contacts the pygal posteriorly, the 11th peripherals posteriolaterally, and the eighth costals anteriorly. There is some variation in the contacts of the eighth costals and adjacent peripherals in Peirópolis A. This is treated above under peripherals.

## Scales of the Carapace

**Vertebrals:** The first vertebral scale in *Bauruemys*, like those of nearly all pelomedusoides, is very wide and thus excludes contact of the first pleural scale with the nuchal bone. The portions of the first vertebral scale that are preserved in *Euraxemys* suggest that this scale was very wide and prevented contact of the first pleural scales to the nuchal bone, however, this remains uncertain. This contact appears to be absent among all podocnemidids (although it may be present in juvenile *Peltocephalus* [P. Pritchard collection]). Among bothremydids, it is absent from all known nuchal bones, except for those of two genera within the Bothremydini for which this region is available, *Chedighaii* and *Araiochleys* (Gaffney et al., 2006). The derived condition is also seen in some species of *Pelusios*.

The shape of vertebral scales varies among these taxa. In *Bauruemys* vertebral scales 2–4 are hexagonal in shape with lateral apexes extending between pairs of pleural scales. Most other podocnemidids are similar, being hexagonal to some degree. However, in most *Lapparentemys* specimens the vertebral scutes have nearly parallel lateral sides (including the type). Only in the referred specimen, MHNC 6904, are they more hexagonal suggesting that this specimen may in fact belong to a different taxon. Recognition of parallel, deep, lateral sulci of the vertebral scales as a character of *Lapparentemys* supports referral of AMNH 14444 to this taxon. The piece of carapace collected with this important skull shows a nearly straight, deep furrow, parallel to the midline that is formed by the vertebral-pleural sulcus.

**Pleuromarginal sulci:** There is some variation in the location of the pleuro-marginal sulcus among podocnemidids. In *Bauruemys* it is generally located about one-third of the distance across the peripheral bones. In *Lapparentemys* and also in Peirópolis A these sulci lie near the middle of the peripherals. In *Cambaremys* and *Podocnemis* this sulcus is nearly coincident with the costo-peripheral suture particularly at the bridge. On the most anterior and posterior peripherals it extends slightly more distally onto the peripherals.

## Bones of Carapace in Internal View

**Axillary buttress:** The axillary buttress in the six taxa of interest shows useful variation in the shape, medial extent and position relative to the suture of the first and second costal bone. In some forms there is contribution of the second costal to the axillary buttress.

In *Cambaremys* and Peirópolis A, the suture for the axillary process of the hyoplastron is nearly uniform in width (fig. 93A; França, 2004: fig. 17; França and Langer,

2005: fig. 5). The suture itself cannot be seen in any of the specimens we consider to represent *Lapparentemys*, but in RM 20.5155 the right hyoplastral process is articulated in place in the carapace and appears to be of equal thickness throughout its contact with the overlying costal and thus seems to represent the same morphology as in *Cambaremys* and Peirópolis A. In Peirópolis B, the suture for the dorsal process of the hyoplastron is wide in the middle part of the first costal but becomes significantly narrowed to a single ridge laterally (fig. 93B). This lateral narrowing of the suture can also be seen in *R. wanderleyi* (MCT 1722-R and the Mezzalira specimen). *Bauruemys elegans* is more difficult to assess, but in the right side of the type, the suture for the hyoplastron on the first costal appears to be reduced to a ridge laterally. Thus, *B. elegans*, *R. wanderleyi*, and Peirópolis B appear to share an alternate morphology of the buttress suture.

In the type of *Roxochelys wanderleyi* (Price, 1953: fig. 3), the medial end of the axillary buttress can be seen to extend medially very close to the midline. It reaches medial to the level of the middle of the first peripheral. A very similar morphology is present in the two specimens we refer to *R. wanderleyi* and in Peirópolis B. In *B. elegans* (holotype and 4348V), *Lapparentemys* (RM 20.5155), *Cambaremys*, and in Peirópolis A, the hyoplastral contribution to the axillary buttress terminates more laterally. It reaches medially to about the middle of the first costal and to the level of the middle of the second peripheral. Medial to the hyoplastral process in all of these taxa, the buttress is composed entirely of the first costal. There is a strong continuous ridge between the hyoplastron buttress and the rib heads that extend to the first and second vertebrae.

Lapparent de Broin and Werner (1998) have noted that in some pelomedusoides the second rib head and axillary buttress are very posteriorly located on the first costal. However, in *B. elegans*, Peirópolis B, and *R. wanderleyi* (best seen in MCT 1722-R), the axillary buttress is supported by thickening of the second costal bone. In these taxa the second costal is thickened, sometimes massively, in the middle of its anterior margin (fig. 93F, G).

In these forms, with the axillary buttress posteriorly located on the first costal the second costal has a slightly curved anterior margin (in ventral view) to accommodate the thickened and posteriorly expanded first costal. Furthermore, the second costal is thickened along its anterior edge, at the point where it is adjacent to the axillary buttress. This can be seen in *B. elegans* (MN 4349-V) and an unnumbered fragment in the DNPM. All three of the specimens that we refer to *R. wanderleyi* show this morphology, as do several first costals of Peirópolis B. This participation of the second costal in the axillary buttress is most developed in *R. wanderleyi*, MCT 1722-R, in which a short process of the second costal extends ventrally posterior to the thickening of the first costal where the latter articulates with the dorsalmost portion of the hyoplastron. In Peirópolis A, *Cambaremys,* and *Lapparentemys*, this contribution to the axillary buttress by the second costal is not present (fig. 93E).

**Inguinal buttress:** In all the taxa described here, the inguinal buttress is formed by a dorsal process of the hypoplastron, which contacts the fifth costal along a suture that is located in the middle of the element. This suture varies in width and medial extent. In Peirópolis A, and *Cambaremys*, this sutural area is wide, 40%–50% of the costal width and limited to the most lateral one-quarter of the costal (fig. 93C). In *B. elegans* (type) and in *Lapparentemys* (RM 20.5155), the inguinal buttress is also very laterally placed. In Peirópolis B, it is narrower and extends further medially extending medially for about one-third of the costal (fig. 93D). *R. wanderleyi* (best seen in Mezzalira specimen, figured in Romano et al., 2009: figs. 2B, 3C) is similar to Peirópolis B.

**Iliac suture:** There is a difference in the sutural attachment of the ilium to the overlying costals seven and eight among the Peirópolis and other species, with two iliac attachment morphologies present (figs. 96, 97). In one, the iliac scar forms a rough oval on costals seven and eight, with the seventh costal scar area being an anterolaterally protruding convexity (figs. 96A, 97A). In the other, the anterior margin of the iliac scar on the seventh costal is an anterolaterally facing concavity. In both the area and

shape of the eighth costal, attachment is roughly similar; it is the shape of the seventh costal sutural surface that differs. Naturally, this difference can be seen in the ilium itself (fig. 96) as well as the carapace (fig. 97). In Peirópolis A the iliac scar is well preserved in two sets of associated coastal bones, seven and eight, one from the left side and one from the right. The scar in these costals protrudes anteriorly (fig. 97D). The medial limit of the scar is defined by a thickened area of bone, mostly on costal eight but extending slightly onto costal seven. This raised block of bone is the site where the rib heads of the sacral vertebrae arise to extend medially to meet their respective vertebral centra. These are thoracic vertebrae 9, 10, and 11, as in a specimen of *Podocnemis erythrocephala* (UF 57921).

In Peirópolis B the iliac scar extends onto the seventh costal both proximally and distally (fig. 98B) suggesting an anteriorly concave ilium (fig. 97B) as in *Podocnemis*. It is not convex anteriorly, as in Peirópolis A (figs. 96A, 97D). The difference in these scars is a result of the shape of the dorsal sutural surface for the ilium. In Peirópolis A it is convex anteriorly, in Peirópolis B; it must be concave anteriorly, as it is in *Podocnemis expansa* (fig. 96B). In the latter, the suture for the ilium crosses from the eighth costal onto the seventh at two sites, one medially and one laterally.

An anteriorly concave scar, like that of Peirópolis B can also be seen in *Cambaremys* (França, 2004: fig. 19) and in *Lapparentemys* (RM 20.5155). In the latter specimen, the dorsal half of the ilium is preserved in articulation with the carapace and can be seen to have an anteriorly concave cross section dorsally. Both the anteriorly concave anterior margin of the dorsal suture of the ilium and the double sutural contact to the seventh costal are on both sides of the Mezzalira specimen of *R. wanderleyi*. In MCT 1722-R both the medial and lateral contacts to the seventh costal are apparent, but the anteriorly concave shape of the suture has been lost due to crushing of the ilium.

The condition of this character is hard to establish in the material of *B. elegans*. Nearly all specimens available to us have the plastron articulated to the carapace and the area of the iliac suture has not been prepared. Only the type is fully prepared in this region, but it is somewhat difficult to interpret. The distal end of the ilium on the left side is preserved in place against the carapace and covers over the sutural area. On the right side, although the ilium is also present, both the anterior and posterior sutures for the seventh costal can be seen for much of the length of this element, but the lateralmost part is missing. The centerline of the seventh costal appears to be thickened, but there is no clear sutural area for the ilium either medially or laterally and the ilium is positioned entirely in contact with the eighth costal. Thus, there is no evidence of an anteriorly concave dorsal suture in the ilium of *B. elegans*.

**Peripherals:** In all but one of the taxa under study, the posterior peripherals are like those of most turtles; there is no internal guttering along the proximal scute sulcus where the marginal scales meet the skin. Peirópolis A appears to possess a unique condition of the posterior peripherals. In this form there is an internal gutter on the ventral surface of peripherals 10, 11, and the pygal, that is deepest on peripheral 11 (fig. 92). This is not seen in any of the other fossil podocnemidids studied and appears to be an autapomorphy for Peirópolis A.

## Plastron

**Bones of plastron:** In the taxa of interest here, the number and arrangement of the plastron elements is relatively uniform as it is among most members of the Pelomedusoides (*Araripemys* and *Pelusios* being notable exceptions). Paired epiplastra and paired hyoplastra enclose a midline entoplastron. Laterally placed mesoplastra are present in all. The paired hyo- and hypoplastra make up the majority of the plastron, and paired xiphiplastra are present as in all turtles. The only variation among these elements is in the relative size of some elements, the scales that cover them (see below), the development of buttresses and the contact of the buttresses to the overlying carapace (described above).

In the Peirópolis material in the DNPM there are two epiplastral morphologies. Most epiplastra in the Peirópolis collections, in-

cluding two pairs that can be associated with Peirópolis A, have a significant rounded lip along the anterior edge. There is a distinct groove just inside the anterior margin that marks the scale overlap by the intergular and gular scales in this form. In a single additional Peirópolis epiplastron, this rolled lip is absent and instead the epiplastron has an angular margin as is seen in *Bauruemys elegans*. This epiplastron we assign to Peirópolis B. There are additional differences between these epiplastral morphologies in the suture with the hyoplastron. In Peirópolis A, the posterior margin at the epiplastron-hyoplastron suture is straight but has a small medial notch for an anterior projection of hyoplastron. In Peirópolis B, instead of a notch there is a significant posteromedial projection extending posteriorly well beyond the lateral part of the suture. This latter morphology is also seen in the type and other specimens of *B. elegans*, and in all three specimens of *R. wanderleyi*. This area is not visible in the type of *Lapparentemys*, in WUS 2160, and is too smashed in RM 20.5155. In MNHN VIL3, there is a posterior projection, but it is very weak, and this specimen shows the distinctively thickened and rounded anterior margin seen in Peirópolis A. In the well-preserved shells from Tiupampa (Broin, 1991), there are also two epiplastral morphologies. The epiplastron is not known in *Cambaremys*.

**Rathke's gland pores:** Much of this material is too poorly preserved to establish the presence or absence of Rathke's gland pores. However, in Peirópolis A, DGM 321 (a specimen with an entire plastron), there is a prominent inguinal pore between the medial edge of peripheral eight and the lateral part of the inguinal buttress. The axillary region of this specimen is also very well preserved and it is clear that there are no axillary Rathke's gland pores, as are present in *Podocnemis*.

**Scales of the plastron:** Although the shell of podocnemidids in general has a highly conserved morphology, one aspect that is variable is the contacts of the scales that cover the anterior plastral lobe as far posterior as the mesoplastra. For these scales we use the traditional terminology of Zangerl (1969) rather than that proposed by Hutchison and Bramble (1981), which differs only in calling the intergular of Zangerl the *gular*, and the gular of Zangerl the *extragular*. Entire anterior plastral lobes are not known for Peirópolis B or *Cambaremys*.

In *Bauruemys*, Peirópolis A, *Roxochelys wanderleyi*, and *Lapparentemys*, an unpaired intergular covers the medial limits of both epiplastra and extends onto the anterior portion of the entoplastron. These contacts are consistent, but there is variation in the width of this scale among the taxa of interest. In the type of *R. wanderleyi* (Price, 1953: fig. 4) and the two referred specimens, this scale is wider than in the other taxa in which this feature is known. In all three specimens, this scale is wider than the adjacent gular. In *Bauruemys*, Peirópolis A, and *Lapparentemys*, as in *Podocnemis*, the intergular width is equal to or smaller than the width of the adjacent gulars. For our purposes, this character is a useful autapomorphy for *R. wanderleyi* but does not appear to be phylogenetically informative.

In the four taxa for which we have plastra, the gulars are relatively small and usually restricted to the epiplastron. In two forms (*Lapparentemys* and some *Bauruemys elegans*) it reaches the entoplastron, but in others (Peirópolis A and *Roxochelys*) it does not. *Bauruemys* shows intraspecific variation with some individuals having gular-entoplastron contact and others not. One specimen, DNPM uncataloged 1969-1, has this contact on the right side but not on the left. In most *B. elegans*, this contact is present.

The humeral scales in *Bauruemys elegans* cover most of the epiplastron, the anterior part of the entoplastron, and a very small anterolateral part of the hyoplastron. In most *B. elegans* the humero-pectoral sulcus extends anterolaterally from the midline across the entoplastron and onto the epiplastron and then near the edge of the plastron turns more laterally to cross the anteriormost part of the hyoplastron (fig. 88). The only exception to this is in DNPM uncataloged 1969-4 in which this suture is more sinuous and crosses onto the epiplastron in two places. The humeral scales meet on the midline in all four of the taxa for which we have plastra, but the length of the contact varies. In *B. elegans* and *Lapparentemys* this midline contact is very short, about ¼ or less of the

length of the entoplastron. In *Roxochelys wanderleyi* and Peirópolis A it is longer, extending ½ or more of the length of the entoplastron. In both of the latter forms this results from more posteriorly place pectoral scales.

The pectoral scale in *B. elegans* covers the anterior part of the hyoplastron and extends anteriorly to cover the posterior half of the entoplastron and a small portion of the epiplastron. Posteriorly, it does not contact the mesoplastron itself but does reach the suture for this bone in some specimens. Laterally it contacts marginal scales four and five. There are no inframarginal scales present. In two of three *Lapparentemys* plastra for which this area is known, contacts of the pectoral scale are identical to *Bauruemys*. In the third (WUS 2160) the pectoral crosses the anterolateral corner of the mesoplastron. Contacts of the pectoral scales in the Mezzalira specimen of *R. wanderleyi* (the only one with complete bridges) are like those of *Bauruemys* in having no mesoplastron contact, but like those of Peirópolis A (both the complete plastron and DGM 321) in not reaching the epiplastra anteriorly. In the complete plastron of Peirópolis A, the pectoral scales cross the anterior part of the mesoplastron clearly on both sides. Thus, mesoplastral contacts of the pectoral scales are similar in *Bauruemys* and *Lapparentemys,* and they differ from the condition seen in Peirópolis A in which they are more posteriorly located.

The presence of the pectoral-abdominal sulcus crossing the mesoplastron appears to be the primitive condition for pelomedusoides. It is clearly seen in *Platychelys*, *Euraxemys*, *Pelomedusa*, *Cearachelys*, "*Galianemys,*" *Chedighaii,* and *Rosasia*. In other taxa this sulcus may lie anterior to the mesoplastron entirely on the hyoplastron as in all podocnemidids, and among the Bothremydidae in *Kurmademys, Polysternon*, and *Araiochelys*; or it may be coincident with the mesoplastron-hyoplastron suture as in all *Pelusios*.

In *Araripemys* the anterior edge of the pectoral scale crosses the anterior lobe of the plastron well posterior to the entoplastron and the epiplastra. This is also the case in *Pelomedusa* and *Platychelys*. In *Euraxemys*, *Pelusios*, *Cearachelys*, "*Galianemys,*" and *Rosasia*, this sulcus crosses the midline of the plastron at or near the suture of the entoplastron with the hyoplastra. In podocnemidids and all known representatives of the bothremydid tribes Taphrosphyini and Bothremydini (other than *Rosasia*), the pectoral sulcus crosses a significant part of the entoplastron.

The abdominal scale in *Bauruemys elegans* is the largest scale in the plastron covering the posterior half of the hyoplastron, the anterior half of the hypoplastron and most of the mesoplastron. It meets marginal scales six and seven laterally, often in a sinuous suture as is also seen in the type of *Lapparentemys*. There is no evidence of an inguinal scale. In Peirópolis A the abdominal scale contacts marginal scales six to eight laterally rather than just marginals six and seven. Furthermore, the posterior margin of the scale is not transverse with respect to the midline but rather angles anteriorly such that it reaches the midline just posterior to the hyo-hypoplastral suture (fig. 91B). Contacts of the abdominal scale in *Lapparentemys* are the same as in Peirópolis A, but the abdominofemoral sulcus is placed further posterior and the midline sulcus more sinuous.

The femoral scales in *Bauruemys* cover the posterior half of the hypoplastron and the anterior half of the xiphiplastron. Anal scales cover the posterior half of the xiphiplastron in all taxa of interest (Peirópolis B is unknown). The only notable variation in these scales among the taxa of interest is the sinuous midline suture seen in the type of *Lapparentemys vilavilensis*.

### Bones of the Plastron in Internal View

If our assumptions are correct and Peirópolis B has straight margins to the anal notch, and that xiphiplastra with a rounded anal notch represent Peirópolis A, then we have material that can be used to describe sutural areas for the pubis and ischium in Peirópolis A. The pubic suture is located midway between the midline and lateral edge. It is oblong, about twice as long as wide, and is oriented at an angle of about 30° from the midline. The ischial suture is more transverse and covers much of the posteriormost part of the xiphiplastron, although it is well offset

from the margin of the bone. The sutural area extends laterally from the midline about two-thirds of the way across the xiphiplastron. The anterior border of the sutural area is straight, the posterior border curves posteriorly, so that the sutural area is about twice as wide laterally as it is medially.

In the Mezzalira specimen of *R. wanderleyi* the internal surface of the xiphiplastron has the distal end of the pubis and ischium still in place. The pubic suture is oval and not as elongate as in Peirópolis A. The ischial suture is narrower than in Peirópolis A. It extends from the midline laterally at a slight angle to transverse. It does not expand laterally as much in this specimen as in Peirópolis A. MCT 1722-R is similar, but the sutures are slightly more robust.

In the type of *B. elegans* the dorsal surface of the xiphiplastron is fully prepared. The pubis is articulated on the left side but not on the right. The sutural area is like that of Peirópolis A, twice as long as wide but at an angle of about 45°. Both ischia are in place and expand both laterally and medially, although the suture itself may be more expanded laterally. This morphology of the ischium differs significantly from that in *Podocnemis expansa*. In the latter, the ischia narrow markedly towards the midline and do not make sutural contact with the xiphiplastra, so that the ischial sutural area on the xiphiplastron does not approach the midline.

In *Cambaremys*, França (2004: fig. 26) has indicated a pubic suture similar to those described above. However, the ischial suture is unusual; it appears to be more L-shaped with a long lateral portion and a narrow section crossing to the midline. In *Lapparentemys* the dorsal surface of the xiphiplastron is visible only in RM 20.5155. The surface of the bone is badly fractured, but it appears that the pubic sutures are larger (longer) than in the other South American forms and oriented at a higher angle to the midline. The ischial suture is similar to Peirópolis A (DGM 321) in that it expands from the midline laterally into a triangular area that is more than twice as wide laterally as medially. Although there is some variation in the sutures for the pubis and ischium, they do not appear to be distinctive enough to be used as scored characters.

### Girdles and Limbs

We can associate disarticulated nonshell postcrania from Peirópolis only on the basis of size. Thus, the larger scapula, possibly representing Peirópolis A, has a dorsal process without a dorsal keel. Peirópolis B has a scapula with a keel present on the dorsal process. The type of *B. elegans* includes both scapulas (left one is complete), left femur, and left humerus; as in *Podocnemis expansa*, the femur is longer than the humerus. In the scapula there is no evidence of expansion or ridges on the dorsal process. However, the acromion process is somewhat flattened as is it in Peirópolis A. In the femur of the type the head extends dorsal to the trochanters to the same degree as in *P. expansa*. In the humerus, the head is very slightly lower than in *P. expansa*.

### Cervical Vertebrae

The most complete specimen of Peirópolis A, DGM 321 has an associated atlas neural arch and centrum and an associated plaster bed for a cervical series. A complete cervical series found in the Peirópolis material is the correct size for DGM 321, but doesn't seem to fit the plaster bed associated in the collection with DGM 321. However, it has the same preservation as the atlas with DGM 321 and consists of cervicals 2–8. In this cervical series number two is biconvex, 3–8 are procoelus. All are generally very similar to *Podocnemis expansa* to which they are compared here. Comparisons are also made to *Erymnochelys madagascariensis* (DGM 279 RR). Cervical 2 has a saddle-shaped condyle. The long ventral keel is longer than that of *P. expansa*. Transverse processes are long in both the fossil and *P. expansa*. Cervical 3 has a distinctly saddle shaped condyle as in *Podocnemis*. In *Erymnochelys* the condyle is very wide and dorsoventrally flattened. Transverse processes are like those in *Podocnemis*, strong and laterally directed. In *Erymnochelys* the processes project slightly more ventrally. In *Podocnemis* the postzygapophyses join to make a single, continuous articular surface. The fossil is more like *Erymnochelys* in this regard. Only the right postzygapophysis is preserved, but it is a

rounded structure, separate from that of the other side. The keel in the fossil is much deeper than in either recent cervical.

Cervical 4 is saddle-shaped posteriorly, much like *P. expansa*. Transverse processes extend laterally as in *P. expansa*, not slightly ventrally as in *Erymnochelys*. Postzygapophyses are united in *P. expansa* and the fossil, but not in *Erymnochelys*. The combined postzygapophyseal surface is constricted medially in the fossil but not in *P. expansa*. Dorsally, the lateral processes of the fossil are connected to prezygapophyses by a broad area of bone making a somewhat winglike structure. The keel is deepest in the fossil. Cervical 5 is saddle shaped like *Podocnemis*. Transverse processes flare slightly upward and are connected to prezygapophyses by a broad expanse of bone. Postzygapophyses in the fossil are barely connected to one another while in *P. expansa* they are strongly connected as in cervicals 3 and 4. Cervical 6 also has a saddle-shaped condyle and broad plates of bone from transverse processes to prezygapophyses. *Erymnochelys* differs from the fossil and *P. expansa* in having the neural spine extend significantly above the postzygapophyses and in having a laterally expanded, convex condyle. Postzygapophyses are not connected in any of the three species. Cervical 7 looks most alike in these three species. The condyle is more balllike in *Podocnemis* and *Erymnochelys*. Postzygapophyses are separate in all three and the neural spine extends dorsal to them. Cervical 8 is like 7 in having a rounded condyle and tall neural arch. The transverse process of *Podocnemis* extends slightly more ventrally than in the fossil.

There are not enough available cervicals for an extensive comparative study among the Podocnemididae at present. These cervicals were found in the same locality as the type specimens of *Pricemys* and *Peiropemys,* but they are most consistent with the larger size of *Pricemys* and Peirópolis A.

## PHYLOGENETIC ANALYSIS

### Previous Work

The early recognition of the enlarged carotid opening (Rütimeyer, 1873; Seibenrock, 1897) in "*Podocnemis*" (sensu lato) might be considered the starting point for recognizing a family level taxon as a monophyletic group, although clearly the literature grouped the living species of "*Podocnemis*" earlier in the 19th century (Pritchard and Trebbau, 1984). The early recognition of three genera in the group (*Erymnochelys* Baur, 1888; *Peltocephalus* Dumeril and Bibron, 1835; as well as the original *Podocnemis* Wagler, 1830) effectively ended with Boulenger's (1889) influential catalog that synonymized the three genera. Later, some authors, including Williams (1954c), Frair et al. (1978), and Gaffney (1979), resurrected these genera to reflect the degree of diversity in the group, and this has become current practice.

Dacqué (1912) and later Zangerl (1948) proposed the first overt phylogenetic hypothesis for what we would now call the Podocnemididae. Although not using these generic names, this was essentially resolved as (*Erymnochelys* (*Podocnemis, Peltocephalus*)), the idea that there was an "African" lineage and a separate "South American" lineage. Although this resolution remained popular, Williams (1954c) questioned this hypothesis and used fossils to argue for what he called the "*Dacquemys-Erymnochelys-Peltocephalus* series," what could be interpreted as (*Podocnemis* (*Erymnochelys, Peltocephalus*)). This is also the hypothesis favored by França and Langer (2006), Meylan et al. (2009), Cadena et al. (2010) and by us. In arguing for his hypothesis, Williams (1954c: 6) states: "In the living species *Peltocephalus dumeriliana* ... the skull has definite, strong similarity to that of *Erymnochelys* or of *Dacquemys* and thus also to the Moghara skull [here named *Mogharemys*]." Later (ibid.: 7) "I differ with Dacqué, Zangerl and others in that I separate from the South American group the species *dumeriliana* ... and regard the few resemblances of the latter species to the other South American forms—similarity in gular pattern and in cervical articulations—as convergent only."

Nonetheless, it was the Dacqué-Zangerl hypothesis that remained popular and was adopted by Gaffney (1988) and Gaffney and Meylan (1988). The first formalization of a podocnemidid phylogenetic hypothesis by naming the subfamilies Erymnochelyinae

and Podocnemidinae was Smith and James (1958). They examined cloacal bursae in turtles and made the following conclusions (1958: 95): "African pelomedusids lack bursae; South American and Madagascar representatives possess them. This distinction, coupled with the presence of saddle cervical joints in the South American group, a deep temporal notch in the African group, and their probable course of isolation, is regarded as significant at the subfamily level; the South American subfamily is designated PODOCNEMINAE (new), the African subfamily the PELOMEDUSINAE of Williams, the Madagascar subfamily the ERYMNOCHELYDINAE (new)." This is the same resolution proposed by Broin (1988 [1989]), and it is clearly the (*Erymnochelys* (*Podocnemis, Peltocephalus*)) hypothesis. These two subfamilies of the Podocnemididae were elaborated and diagnosed by Broin (1988 [1989]): the subfamily Podocnemidinae and the subfamily Erymnochelinae (also see discussion in Systematics section). Although used in a number of additional papers (Broin, 1991; Lapparent de Broin, 2000a, 2001, 2003a, 2003b), the most complete expression of the hypothesis is Lapparent de Broin (2000b) as follows: "Subfamily Podocnemidinae" (sensu Broin, 1991)—*Podocnemis, Peltocephalus, Bauruemys,* aff. *Roxochelys vilavilensis* [here named the new genus *Lapparentemys*], *Stupendemys*. The character that seems to be dominant in Lapparent de Broin (2000b, and other papers) for this taxon is the saddle-shaped cervicals (see also Character Descriptions for a different interpretation), but, as in the case of Smith and James (1958), biogeography is also used as a dominant phylogenetic character. There are a series of shell characters as well, but the distributions are not consistent. Apparently, the fact that *Bauruemys* lacks the cervical character was not yet known and the author used various shell features and geography to place this species in this group. In our analysis, this subfamily is simply a paraphyletic group of South American podocnemidids.

"Subfamily Erymnochelinae" (sensu Broin, 1991)—*Erymnochelys, Neochelys, Stereogenys, Shweboemys, Dacquemys, Carteremys*. This group is essentially the present authors' magnatribe Erymnochelydand. The reflection of the cladogram in the classification requires its change in category, otherwise we would have kept the original name; we agree with most of its content and principle characters. The primary character used for this group (Lapparent de Broin, 2000b: 70) is the "Much eroded roof of the enlarged carotid canal, the prootic and quadrate being so much eroded that the floor of the canalis cavernosus is broken and this canal is anteriorly confluent with the part of 'enlarged canal' leading to the sulcus cavernosus (not known in *Dacquemys*, homoplastic but with a less eroded roof in the podocnemidine *Peltocephalus*). The interesting recognition by Lapparent de Broin (2000b) that the character does actually occur in *Peltocephalus*, a member of the other subfamily, does not escape the author, but the geographic consideration is too great. There are now a few cervicals showing that members of Lapparent de Broin's Erymnochelyinae did have saddle-shaped centra.

The advent of nonmorphological characters has produced results inconsistent with either of the two morphological Podocnemididae hypotheses developed over the past century. Frair et al. (1978) produced a resolution of: (*Erymnochelys* (*Peltocephalus* (*P. expansa, P. vogli, P. lewyana, P. unifilis, P. erythrocephala* (*P. sextuberculata,*)))) based on a serological analysis. The Frair (1980) serologic study emphasized chelids and only concluded that *Peltocephalus* and *Erymnochelys* were distinct from *Podocnemis*. The karyologic study of Rhodin (1978) also concluded that *Peltocephalus* and *Erymnochelys* were distinct from *Podocnemis*. When just considering the Recent genera, none of the molecular results reproduce the Dacqué (1912), Zangerl (1948), Gaffney (1988), Gaffney and Meylan (1988), and Lapparent de Broin (2000b) resolution of (*Erymnochelys* (*Podocnemis, Peltocephalus*)), or the Williams (1954c) and França and Langer (2006) hypothesis of (*Podocnemis* (*Peltocephalus Erymnochelys*)); rather they present the hypothesis advanced by Frair et al. (1978), the (*Peltocephalus* (*Podocnemis Erymnochelys*)) arrangement.

Molecular analyses of the Podocnemididae first only resolved generic level taxa (Seddon et al., 1997; Georges et al., 1998; Noonan, 2000; Noonan and Chippendale, 2006) and

presented the following resolution: (*Peltocephalus* (*Podocnemis Erymnochelys*)). A later molecular study (Vargas-Ramírez et al., 2008) was the first to include all the Recent Podocnemididae species, and supported the earlier resolution of the genera. It is interesting that the molecular studies have agreed on an alternative that has not been expressed by any of the earlier morphologic analyses. So all three possible outcomes for resolving the three living genera are supported by some study.

It should be noted that the topology of the species resolution in the Vargas-Ramírez et al. (2008: fig. 3) molecular study has almost nothing in common with our resolution of species based on morphology. Although we feel that we have relatively strong support for the union of *Peltocephalus* and *Erymnochelys*, we do not have similar optimism about our resolution of the species within *Podocnemis*. The characters used are frequently subject to homoplasy in other turtle taxa, but, osteologically speaking, these Recent species are very similar to each other. Some are not even readily identifiable from skeletal parts alone, hence the low confidence in our resolution of the *Podocnemis* species.

## Character Descriptions

**1. NA, nasal:** (0) present; (1) absent.

*Discussion:* See Gaffney et al. (2006).

**2. FR, orbital position:** (0) facing laterally, anterolaterally; (1) facing dorsolaterally; (2) facing dorsally.

*Discussion:* The difficulty in using characters like this one is distinguishing discrete characters that are actually gradational, therefore making them even more subjective than usual. The problem is discussed in Gaffney et al. (2006: 577). See also Meylan et al. (2009: 10). For the restricted group of the Podocnemididae we felt that this was possible because there is not that much individual or specific variation among the living forms and a number of the fossils are definitive in their morphology. State 2 only occurs in *Bauruemys*. State 1 is primitive for the family.

**3. FR, interorbital groove:** (0) absent; (1) present.

*Discussion:* The narrow groove in the narrow interorbital bar formed by the dorsal surface of the prefrontal and frontal in all the living species of *Podocnemis* and the extinct *Podocnemis bassleri* (Williams, 1956) is a good synapomorphy for this genus. Williams (1954a) used this character for *Podocnemis*.

**4. FR, prefrontal and frontal in lateral view:** (0) flat or slightly convex; (1) strongly convex dorsally.

*Discussion: Bairdemys* (except *B. winklerae*) differs from the other tribe Stereogenyini in having a pronounced bulge in the skull roof between the orbits resulting in a markedly attenuated preorbital region. The other members of the tribe Stereogenyini have flat or less pronounced profiles. This character is approached outside the tribe Stereogenyini by *Podocnemis* (Gaffney, 1979: fig. 134), and *Bairdemys* is still more extreme. See Gaffney et al. (2008) for further discussion. Although this character is rare in pleurodires, a convex interorbital profile occurs in sea turtles and batagurids. The simple morphology of the character makes homoplasy testing difficult.

**5. PAR, quadratojugal-parietal contact:** (0) absent; (1) short contact; (2) long contact.

*Discussion:* Gaffney et al. (2006: 578) discusses this character. See also Fuente (2003) and França and Langer (2006: 371).

**6. PAR, parietal-pterygoid contact in septum orbitotemporale:** (0) absent; (1) present and wider; (2) present and narrower.

*Discussion:* The septum orbitotemporale and its associated sulcus palatinopterygoideus are described and figured in Gaffney et al. (2006: 118–126, figs. 23–25). The wider parietal-pterygoid contact unites the tribe Stereogenyini with *Neochelys*.

**7. PAR, temporal emargination:** (0) moderate to absent; (1) extreme, as in *Pelusios;* (2) shallow, cheek emargination extending posterodorsally to or above quadrate; (3) emargination absent due to expanded parietal/supraoccipital.

*Discussion:* Many authors have used temporal emargination as a character. It is a gradational feature, hard to make objective, and highly subject to homoplasy. França and Langer (2006: 371) use criteria that are as good as any, but here we have taken a more extreme view. We distinguish only the

relatively narrow postorbital roofing present in Pelomedusidae and *Araripemys* as one state and all others that are more roofed as a single state. Certainly such conditions as found in *Bauruemys* and *Bairdemys sanchezi* are more emarginate than *Cordichelys* and *Dacquemys*, but we have not tried to tease out the various conditions.

State 2 characterizes chelids that retain parietal-squamosal contact, except in *Chelodina* (contact lost due to extensive cheek emargination, not temporal emargination). State 3 seeks to unite the skull roofing morphology seen in *Dacquemys* (Gaffney et al., 2002) with an as yet undescribed specimen from the Lake Turkana Miocene, UCMP 42008 (see Systematics section). The character is a completely covered temporal roof caused by the large posterior part of the parietal with some lateral expansion of the supraoccipital.

**8. PAR, interparietal scale:** (0) absent; (1) equilateral triangle; (2) elongate triangle; (3) parallel sided; (4) broad posteriorly.

*Discussion:* Williams (1954a: 284) used the head scalation of podocnemidids and we have attempted to use these features. See also Meylan et al. (2009: 11). There is a great deal of homoplasy in the distribution of the states, however. State 1 appears to be primitive for the family Podocnemididae and state 3 appears to be a subtribe Stereogenyina synapomorphy. *Turkanemys* could be considered trapezoidal (Wood, 2003), but it seems to us as very similar to the equilateral triangle condition.

**9. JU, jugal-quadrate contact:** (0) absent; (1) present.

*Discussion:* This is the classic character that unites *Peltocephalus* and *Erymnochelys* (Baur, 1890; Williams, 1954c; Siebenrock, 1897, 1902) in contrast to *Podocnemis* among the living fauna. But it is still a nearly unique character when viewed from the context of the fossil record. Only the heavily roofed UCMP 42008 also has this character, and there is some morphologic reason to think that they are not homologous. The cheek of UCMP 42008 has a number of bone contacts that differ from *Erymnochelys* and *Peltocephalus*, and its sister taxon, *Dacquemys*, has no jugal-quadrate contact. So this does appear to be a synapomorphy for *Peltocephalus* + *Erymnochelys*, despite the fact that it is homoplastic in other turtle groups (Gaffney, 1979).

This character may occur in an undescribed specimen, KNM-RU 18401 (Witmer, 1990), from the Miocene of Rusinga Island, Kenya (see discussion above under *Turkanemys*).

**10. JU, jugal-parietal contact:** (0) absent; (1) present.

*Discussion:* The jugal-parietal contact unites the recent species of *Podocnemis* (and *P. bassleri*) due to the very small postorbital bone characteristic of this genus (Ruckes, 1937; also in Gaffney, 1979). There is no homoplasy known.

**11. JU, Cheek emargination:** (0) slight; (1) reaches level of orbit; (2) reaches above level of orbit; (3) reaches above quadrate.

*Discussion:* Cheek emargination, like temporal emargination is basically a gradational character that needs to be broken up into states that are as objective as possible. Our interpretation of states is described and discussed in Meylan et al. (2009: 11). State 1 is primitive for podocnemidids in our analysis with state 2 diagnostic for the *Peiropemys* + *Lapparentemys* + *Pricemys* grouping.

Cheek emargination in the subtribe Stereogenyina is determinable only in *Bairdemys*, *Stereogenys*, and *Cordichelys*. In *Bairdemys* the emargination is most extensive and very similar in size and shape to *Podocnemis*. *Stereogenys* has a slight, nearly absent emargination with *Cordichelys* appearing to be intermediate, although it could be more extensive. Skull roof emargination is variable in turtles, and other podocnemidids, *Peltocephalus* and *Erymnochelys*, have closed cheeks, although the bones involved (Gaffney, 1979) differ from the subtribe Stereogenyina.

**12. SQ, ventral vertical flange:** (0) absent; (1) present.

Discussion: This character seems to be an attachment area for the M. depressor mandibulae (see Gaffney et al., 2006: 582, for discussion in bothremydids). Small squamosal flanges occur variably in *Podocnemis expansa, Peiropemys, Lapparentemys,* and *Bauruemys,* but for this character we distinguish the distinct and deep flange that

characterizes the species of *Bairdemys* (see also Gaffney et al., 2008).

**13. PO, size:** (0) equal to orbit; (1) smaller than orbit.

*Discussion:* The unusually small postorbital in *Podocnemis* has been described before (Ruckes, 1937; also in Gaffney, 1979), but we have seen specimens of *P. unifilis* that have a more normal sized postorbital, a presumed reversal in our analysis. The character does not occur elsewhere.

**14. PM, premaxillae reach apertura narium interna:** (0) no; (1) yes.

*Discussion:* State 1 may include two states, depending on interpretation, as always. The subtribe Stereogenyina have a well-developed secondary palate with a midline cleft. The position of the apertura narium interna is somewhat arbitrary, as it could be considered to lie at the anterior end of the cleft or at the posterior end of the secondary palate, its position in other turtles with secondary palates, such as cheloniids. In this case, we have interpreted the midline cleft as constituting the apertura narium interna. We base this on the purely morphologic condition that the premaxillae have a free posterior edge in the subtribe Stereogenyina as they do in *Neochelys, Peltocephalus*, and *Erymnochelys.* This interpretation results in a grouping of the subtribe Stereogenyina with *Neochelys, Peltocephalus*, and *Erymnochelys.*

However, it is possible that the cleft was covered with soft tissue, not preserved, and the apertura narium interna would be more posterior. The more posterior position is also more likely than the thin cleft as a pathway for incoming air, if one were to use a more physiologic interpretation. If one were to consider the subtribe Stereogenyina condition as an alternate state, then it would provide another synapomorphy for the subtribe Stereogenyina and remove one uniting the three previously named genera. Take your pick.

**15. PM, pinched snout:** (0) absent; (1) concave outline near premaxilla-maxilla contact, snout not elongated; (2) concave outline posterior to premaxilla-maxilla contact, snout elongated.

*Discussion:* This character is relevant to the subtribe Stereogenyina. It was used by Gaffney and Wood (2002), criticized by Sánchez-Villagra and Winkler (2006), and defended (or further confused) by Gaffney et al. (2008). See the latter publication for further discussion and possibly more precise description. As presently interpreted, the pinched snout in all its magnificence occurs in the infratribe Stereogenyita (not known in *Brontochelys*) and in *Peltocephalus. Bairdemys winkleri* has a unique elongated snout with a broadly concave outline that we do not interpret as the same state as in the infratribe Stereogenyita. However, this is a morphologically simple character, whose homology is difficult to test for, and it is found widely homoplastic throughout turtles. Other podocnemidids usually have straight snouts, so the pinched condition is presumably derived.

**16. MX, medial expansion of triturating surface:** (0) absent; (1) present, forming median maxillary ridge; (2) secondary palate with midline cleft.

*Discussion:* The palates of *Bauruemys, Peiropemys, Lapparentemys*, and *Pricemys*, as well as the outgroups to the Podocnemididae, *Hamadachelys, Portezuelemys*, and *Brasilemys*, all have the anterior part of the palate with a wide concavity on the midline, formed by the premaxillae and anterior part of the maxilla. This concavity is related to the relatively narrow anterior (and sometimes posterior as well) part of the triturating surface, formed mostly by the maxilla. In the remaining Podocnemididae, with the exclusion of the subtribe Stereogenyina, the anterior part of the maxilla is medially expanded, usually in the form of a variably developed ridge, the median maxillary ridge. The median maxillary ridge extends "the length of the maxilla along the middle of the triturating surface and then extends onto the premaxilla anterior and ventral to a well-defined foramen praepalatinum" (Meylan et al., 2009: 13). The medial expansion of the maxilla constricts the midline concavity, reducing it to a short trough.

In the present analysis the medial expansion of the maxilla is an important character that defines the group consisting of *Podocnemis* + infrafamily Erymnochelyodda with a secondary modification in the subtribe Stereogenyina. The palate in the subtribe Stereogenyina is highly modified, but the

presence of the medial expansion in the maxilla can be considered as the anterior part of the secondary palate. The medial expansion of the maxilla is relatively variable within cryptodires. Thus, the consistency of this character within the Podocnemididae is interesting and somewhat unexpected.

Character state 2, the complete secondary palate formed by maxilla and palatine, is a very distinctive feature of the subtribe Stereogenyina and does not occur outside that group. A number of turtles have evolved secondary palates; some like *Osteopygis* (Gaffney, 1979) are more extensive than in the subtribe Stereogenyina. But all other chelonian secondary palates have the bones meeting in the midline, usually with contributions from the vomer, often with a vomerine pillar dorsally, separating the two choanal passages (Gaffney, 1979). The subtribe Stereogenyina are unique among turtles in having a secondary palate with a median cleft and no contribution from the vomer, which is absent in the group. The posterior extent of the secondary palate varies in the subtribe Stereogenyina, but the width of the median cleft is relatively constant. There is no way to determine whether or not the cleft was filled in life with cartilage or soft tissue or whether it allowed the passage of incoming air. The morphologic consistency and the unique distribution of the median cleft support the homology of this character among the subtribe Stereogenyina.

**17. MX, secondary palate long:** (0) no, relatively short (palate length/skull length less than 0.6); (1) yes, relatively long (palate length/skull length more than 0.7).

*Discussion:* In *Stereogenys* the ratio of palate length to skull length varies among four specimens from 0.71 to 0.73 and in *Shweboemys* the ratio is 0.68. These are relatively long palates. The shorter palates represented by the other taxa range from 0.47 (*Brontochelys*) to 0.58 (*Cordichelys*). We interpret the shorter palates as primitive only because the outgroups lack secondary palates. The larger secondary palate of *Stereogenys* and *Shweboemys* is made up of a relatively larger palatine bone when compared with the other subtribe Stereogenyina.

**18. MX, triturating surface convexity:** (0) absent or shallow; (1) deep.

**Discussion:** Two species of *Bairdemys, B. venezuelensis* and *B. hartsteini,* differ from the other subtribe Stereogenyina in the large size of the palatal swellings. *Latentemys* and *Cordichelys* also have these swellings, but they are not as large or pronounced as in these species of *Bairdemys.*

**19. MX, labial ridge:** (0) high and narrow; (1) low and thick.

*Discussion: Stereogenys*, *Shweboemys*, *Lemurchelys*, and *Brontochelys* have relatively low and thick labial ridges in contrast to the other subtribe Stereogenyina.

**20. MX, accessory ridges:** (0) absent; (1) one or two.

*Discussion:* See Gaffney et al. (2006: 587) and Meylan et al. (2009: 13) for discussion and description. There is some homoplasy in this character in our analysis. It occurs in *Podocnemis* + infrafamily Erymnochelyodda, with the exception of *Neochelys,* and a reversal for the subtribe Stereogenyina. The absence of any ridges in the subtribe Stereogenyina is a synapomorphy of that group.

Williams (1956: 4) describes the ridges in *Podocnemis expansa* and *Podocnemis bassleri*: "(1) a short anterior ridge beginning on the premaxilla and extending a short distance onto the maxilla; (2) a ridge parallel to this beginning at the premaxillary suture and extending posteriorly almost to the end of the triturating surface; (3) a broad roughened area parachoanal in position, converging anteriorly towards the second ridge, not parallel to it. This third ridge or roughened area is very low and broad in the fossil, as it is occasionally in *P. expansa.* In the fossil there is no evidence of the faint ridge on the internal surface of the tomium which is regularly present in *P. expansa.*"

**21. MX, meet broadly on midline:** (0) no; (1) yes.

*Discussion:* Descriptions of this character can be found in Gaffney et al. (2002: 10) and Meylan et al. (2009: 13). In the present analysis, the midline meeting of the maxillae is completely homoplastic, occurring independently four times, forming no groups.

**22. VO, vomer:** (0) present; (1) absent.

*Discussion:* The presence/absence of the vomer in the Podocnemididae requires multiple losses in our analysis. The vomer has been lost three times within the Pelomedu-

soides, once in the Pelomedusidae plus *Araripemys* (the magnafamily Pelomedusera of Gaffney et al., 2006), once within *Podocnemis*, and once within the Infrafamily Erymnochelyodda, as the vomer is absent in all of that clade except *Caninemys* (Meylan et al., 2009: 13). The very thin, barely recognizable, vomer in *Podocnemis vogli* could be interpreted as a neomorph as its morphology has very little in common with the vomer in the outgroups. It is identified on the basis of its position rather than its morphology.

**23. PAL, medial edges of palatal cleft:** (0) absent; (1) medial edges parallel; (2) medial edges curved.

*Discussion:* In *Stereogenys, Lemurchelys,* and *Shweboemys* the medial edges of the palatal cleft are parallel to each other. In the other genera of the subtribe Stereogenyina they are curved, convex toward the midline. In the absence of an outgroup with a secondary palate, it is impossible to determine which (if either) condition is primitive or derived. The parallel-edged condition is found in the same taxa that have the longest secondary palate and it is possible that these are functionally associated in some way. In any case, the sister taxon relations of *Stereogenys, Lemurchelys,* and *Shweboemys* are supported by other characters.

**24. PAL, palatine extent in triturating surface:** (0) narrow or absent; (1) moderate, but much less than extent of maxilla; (2) large, equal to or slightly less than extent of maxilla.

*Discussion:* This character is somewhat gradational, and we have separated out the most extreme condition, that of the secondary palate in the subtribe Stereogenyina, as a second state. State 1 is a synapomorphy for the Podocnemididae.

**25. PAL, dorsal process of palatine contacts parietal in septum orbitotemporale:** (0) no; (1) yes.

*Discussion:* The septum orbitotemporale and its associated sulcus palatinopterygoideus are described and figured in Gaffney et al. (2006: 118–126, figs. 23–25). *Shweboemys* has a large process of the palatine that rises dorsally in the septum orbitotemporale to form much of the septum. It contacts the parietal posterodorsally and is interposed between the jugal and the pterygoid laterally and the postorbital and the pterygoid medially.

In *Stereogenys* this palatine process can be seen in BMNH R.3191. In this specimen the palatine-parietal and palatine-pterygoid sutures show the posterior and dorsal extent of the palatine, but the anterior and anterodorsal contacts with the jugal and postorbital are obscured. None of the other *Stereogenys* specimens are well enough preserved to determine sutures in this area. In other subtribe Stereogenyina and other podocnemidids the palatine forms only the ventral edge of the fossa temporalis and the jugal and pterygoid meet to form the septum orbitotemporale.

**26. PAL, dorsal process of palatine contacts frontal in septum orbitotemporale:** (0) no; (1) yes.

*Discussion:* The dorsal palatine process is in the anterior margin of the septum orbitotemporale. The frontal sends a process ventrally to meet the dorsal process of the palatine about halfway up the height of the wall. The septum orbitotemporale and its associated sulcus palatinopterygoideus are described and figured in Gaffney et al. (2006: 118–126, figs. 23–25). This character is a synapomorphy for the tribe Stereogenyini, which is the subtribe Stereogenyina plus *Mogharemys.*

**27. PAL, fossa orbitalis posterior pocket in septum orbitotemporale:** (0) absent; (1) present.

*Discussion:* The subtribe Stereogenyina are characterized by a relatively thick septum orbitotemporale separating the fossa orbitalis from the fossa temporalis. The anterior surface of the septum orbitotemporale is an anteriorly facing concavity, presumably containing eyeball attachments or orbital glands. None of the other Pelomedusoides have this concavity. The concavity occurs in all the subtribe Stereogenyina that have this area exposed. However, *Shweboemys* and *Bairdemys winkleri* have matrix filling the two specimens representing this taxon, so the distribution of this character is not definite.

**28. PAL, basisphenoid-palatine contact separates pterygoids:** (0) no; (1) yes.

*Discussion:* In *Shweboemys* the basisphenoid separates the unusually small pterygoids to barely contact the palatines just on the

midline. Some of both pterygoids and basisphenoid have been eroded off the surface, but the original positions of the sutures seem to have had a basisphenoid-palatine contact. *Stereogenys* also has basisphenoid-palatine contact. BMNH R.3191 is the only *Stereogenys* specimen clearly showing the basicranial sutures. In this skull the elongate basisphenoid completely separates the pterygoids, to a greater extent than in *Shweboemys*, and broadly contacts the palatines, partially separating them, also in contrast to *Shweboemys*. The basisphenoid-palatine contact does not occur in other pleurodires.

**29. QU, antrum postoticum:** (0) large; (1) smaller; (2) smallest and slitlike.

*Discussion:* In most pleurodires (and cryptodires) the antrum postoticum is a cone-shaped cavity formed by the squamosal and communicating with the cavum tympani of the quadrate. In *Bairdemys* (unknown in *B. winkleri*), *Lemurchelys,* and *Stereogenys*, however, the antrum is collapsed to a small slit and contains almost no space. This is in contrast to the relatively open antrum seen in *Latentemys* and *Cordichelys*. Unfortunately, the region is missing in *Shweboemys* and *Brontochelys*. *Caninemys* also has a very small antrum, not quite the slit seen in the subtribe Stereogenyina, but we have coded it as state 2. In our analysis, state 2 appears three times independently.

**30. QU, fossa precolumellaris:** (0) very small to absent; (1) present but shallow; (2) deep and well defined.

*Discussion:* See discussion in Gaffney et al. (2006: 600). In our analysis, we have used three states to express this character. We do not order them, however, it is hard to see, transformationally speaking, how state 0 (small or absent) could reach state 2 (deep) without going through state 1 (shallow). The rather diverse distribution of this messy character has inclined us to make as few assumptions as possible. Consistent with earlier analyses (e.g., Fuente and Iturralde-Vincent, 2001; Fuente, 2003; Gaffney et al., 2006; Meylan et al., 2009) our analysis shows that the deep and well-defined state is primitive for the Eupleurodira at least, although we have scored the absent condition as primitive because it is absent in *Proganochelys* and other non-casichelydian turtles.

**31. QU, eustachian tube separated by bone from fenestra postotica:** (0) no; (1) yes.

*Discussion:* The fenestra postotica (Gaffney, 1979: figs. 85–102) of turtles is very variable in the degree to which structures traversing it are delimited by bone. In *Bairdemys* and *Latentemys* there is a bony wall subdividing the fenestra postotica that is not found in any other turtles. The wall appears to separate the Eustachian tube from the lateral head vein (vena capitis lateralis).

**32. QU, incisura columellae auris:** (0) no posterior bony restrictions; (1) eustachian tube separated from stapes by bone or narrow fissure; (2) eustachian tube and stapes enclosed or nearly enclosed by bone.

*Discussion:* State 2 is a synapomorphy for the family Podocnemididae plus *Hamadachelys,* but is unfortunately unknown for *Portezuelemys*. Further discussion in Gaffney et al. (2006) and Meylan et al. (2009).

**33. QU, quadrate-basioccipital contact:** (0) absent; (1) present.

*Discussion:* See Gaffney et al. (2006) for discussion. This character (among others) unites the superfamily Podocnemidoidea, essentially the family Bothremydidae plus epifamily Podocnemidinura.

**34. QU, medial quadrate process reaches braincase:** (0) absent; (1) present.

*Discussion:* See Gaffney et al. (2006) for discussion.

**35. PT, cavum pterygoidei:** (0) absent; (1) partial; 2) complete.

*Discussion:* Rütimeyer (1873: 58–62) seems to have been the first to describe the enlarged carotid opening in *Podocnemis,* and we have been unable to find an earlier statement. Seibenrock (1897) described it in detail for *Erymnochelys madagascariensis*. Siebenrock's description (1897: 301, 302; given here in translation from the German courtesy of B. Werscheck) is worth repeating at this point:

> In *Podocnemis* [*Erymnochelys madagascariensis* is the species Seibenrock, 1897, figured in pl. 6, fig. 38, and is presumably the one he describes below] the canalis caroticus internus is unusually widened, and Rütimeyer very fittingly compared it to a bony funnel. Rütimeyer states that from an osteological point of view the reason for this shape cannot be explained, but goes on to say 'that it could have something to do with the blood supply and/or discharge to and from the

> brain and the eyes,' and that it was probably for the blood vessels of the carotids and jugulars. The latter is quite right, but even for this the canal does not have to be that wide. If you look at the canal closely you can see four holes that indicate either the start or the termination of four canals. At the medial wall, behind the otosphenoideum [= prootic], we find the foramen for the lower branch of the nervus facialis, which unites with the nervus vidianus, which is moving forward in the canalis caroticus internus. Slightly more towards the front of the basisphenoideum we find the foramen, which leads the carotis interna towards the base of the brain and which terminates in the fossa hypophyseos in the cranial cavity. At the roof of the second canal we find the foramen for the anterior branch of the carotis externa, which is led through the recessus cavi tympani into the cranial cavity and from there to the eye. Finally the nervo vidiano comes through the floor of the pterygoideum through the foramen pro ramo nervo vidiano, enters into a canal and terminates at the upper surface of the pterygoideum behind the orbital cavity and medial to the foramen palatinum posterius. The canalis caroticus externus is the only canal that starts in the recessus cavi tympani, and above, it is between the otosphenoideum and the quadrate, together with the carotico-temporale, and they terminate into the wide canal. The canalis cavernosus, which normally terminates here in the turtles, is missing. Therefore, we can assume that in *Podocnemis* the vena jugularis interna and the nervus facialis move through the widened canalis caroticus internus. Judging from the size of the foramina for the carotids, one can see that they are not abnormally large, therefore, only the venous system seems to be much more developed than normally. However, the question now arises of why is it only in *Podocnemis* that the venous system is so much larger than the arterial system. Therefore, the width of the canal must have other reasons as well, but these can probably only be determined in a recently killed animal.

The "enlarged carotid canal" has been and is used by many previous authors as a character. The term "cavum pterygoidei" is a more formalized name for the "pterygoideus muscle chamber" or "enlarged carotid channel" of Gaffney (1979: fig. 86) and others. First formalized by Gaffney and Wood (2002: 20) as the cavum pterygoideus, it was changed for no reason to cavum pterygoidei in Gaffney et al. (2006: 603). State 2 is hypothesized as diagnostic for the family Podocnemididae, as it has been for over 100 years (Rütimeyer, 1873; Siebenrock, 1897, 1902).

The cavum pterygoidei is a relatively large opening from the palate into the braincase located at the posterior end of the pterygoid, containing a subdivision of the pterygoideus muscle (Schumacher, 1954, 1955a, 1955b, 1973). It is differentiated from the fossa pterygoidea found in bothremydids (Gaffney et al., 2006) by having at least a partial covering ventrally and an anteromedial opening into the braincase. The two sister groups of the Podocnemididae, *Brasilemys* (Lapparent de Broin, 2000b) and *Hamadachelys* (figs. 1–6; Tong and Buffetaut, 1996), have a cavum pterygoidei that is hidden anteromedially by the underlapping basisphenoid medially and the pterygoid laterally. In these taxa the cavum is not as deep as in all other Podocnemididae, but the cavum pterygoidei is interpreted here as homologous in *Hamadachelys*, *Brasilemys*, and Podocnemididae. The partial condition in *Brasilemys, Hamadachelys,* and *Portezuelemys*, is interpreted as additive to the complete state.

The cavum pterygoidei (for contents see Siebenrock, 1897; Albrecht, 1976; Gaffney, 1979; Schumacher, 1954, 1955a, 1955b, 1956, 1973), in its completely developed state, is formed by four bones: the basisphenoid anteriorly and medially, the pterygoid ventrally and laterally, the prootic posterodorsally, and the quadrate posterodorsolaterally. There are five foramina in the cavum pterygoidei in *Pricemys* and *Peiropemys*. Posteromedially along the length of the basisphenoid is the foramen nervi abducentis (1). More anteriorly, also within the basisphenoid, near the anterior limit of the cavum pterygoidei is the foramen posterius canalis carotici interni (2); just lateral to this is the foramen caroticum laterale (3). The pterygoid-basisphenoid suture is lateral to the foramen caroticum laterale, and lateral to that contact and within the pterygoid is the foramen nervi vidiani (4). More posteriorly in the cavum, in its dorsal surface, the prootic is exposed. The foramen nervi facialis (5) lies in the center of the prootic. The foramen nervi vidiani is frequently hard to find as it is usually very small.

These foramina can be probed in the braincase of *Pricemys*, which has had nearly all the matrix removed in the cavum cranii and both cava pterygoidei. *Bauruemys* MCT 1753-R (figs. 11, 12) has the cavum pterygoidei exposed on both sides. Here the foramen posterius canalis carotici interni appears to be combined with the foramen caroticum laterale as one oval opening, possibly damaged by preparation. So this specimen has four foramina comparable in position to those in *Pricemys* and *Peiropemys*. Unfortunately, none of the *Roxochelys* specimens are as well preserved or as matrix-free as the *Pricemys* and *Peiropemys*, but the areas preserved agree with the *Pricemys* and *Peiropemys* morphology. The skull figured in Broin (1991: pl. 2, figs. 1–7, "Tiupampa"), which is *Lapparentemys vilavilensis* and not the shell genus, *Roxochelys*, has nearly all of the cavum preserved on one side or the other, and it has the *Pricemys* and *Peiropemys* condition.

This character is used by Gaffney and Meylan (1988), Meylan (1996), Lapparent de Broin and Werner (1998), Lapparent de Broin (2000b), Fuente and Iturralde-Vinent (2001), Fuente (2003), and Gaffney et al. (2006), among others, and has been used since Rutimeyer (1873), Siebenrock (1897, 1902), and later Williams (1954a).

**36. PT, anterior opening of cavum pterygoidei:** (0) absent (cavum pterygoidei absent); (1) small opening; (2) moderate opening; (3) large opening, foramen cavernosum opens in roof of cavum pterygoidei.

*Discussion:* The anterior opening of the cavum pterygoidei has what we have identified as three states. In the most primitive condition the foramen caroticum laterale, foramen anterius canalis carotici interni, and foramen nervi abducentis are small foramina, but the cavum pterygoidei anterior wall is otherwise a solid wall of bone formed by the basisphenoid, pterygoid. and prootic. The canalis cavernosus does not communicate with the cavum in any way. In the morphologically intermediate condition, both the foramen posterius canalis carotici interni and the foramen anterius canalis carotici interni are much larger; the more posterior foramen nervi abducentis is very large and its anterior opening is part of the large foramen anterius canalis carotici interni. The wall formed by the pterygoid ventrally and the prootic dorsally is eroded away to some extent in this intermediate condition, making the canalis/sulcus cavernosus open to the more ventral cavum pterygoidei.

In the most extreme condition, state 3, this prootic/pterygoid wall is absent and there is no contact between them in the anterior region of the cavum pterygoidei. The canalis cavernosus is more posteriorly placed and is an opening in the prootic-quadrate suture in the dorsal surface of the cavum pterygoidei near the foramen nervi facialis. In this condition there is no demarcation between the cavum pterygoidei proper and the sulcus cavernosus; presumably the lateral head vein runs anteriorly with the other structures exiting the cavum pterygoidei. We interpret the large opening state as distinct from the character "foramen cavernosum opens in roof of cavum pterygoidei." However, these characters may not be independent. Nonetheless, we have run the analysis with the latter character removed and the result is the same.

Described by Lapparent de Broin (2000b), the opening of the canalis cavernosus/foramen cavernosum into the roof of the cavum pterygoidei is a character that differentiates the living *Podocnemis*, which lack it, from *Peltocphalus* and *Erymnochelys*, which have it (see discussion above under Sysytematics for *Erymnochelys*). However, Lapparent de Broin (2000b) prefers an alternate phylogenetic hypothesis, uniting *Podocnemis* and *Peltocphalus*, by arguing that the occurrence of this character in *Peltocephalus* is homoplastic. She states that there are some differences in position of the foramen cavernosum in *Peltocephalus* and *Erymnochelys*, and that *Peltocephalus* agrees with *Podocnemis* in geography and the possession of saddleshaped cervical centra, absent in *Erymnochelys*. In addition, Broin (1991: 513) explains that in *Erymnochelys* and *Neochelys* the "inner surface of the canalis caroticus is also much enlarged but differently" from the condition in *Peltocephalus* and *Podocnemis* and gives a description. This statement agrees with our observations as well, and the entry of the carotid artery into the basisphenoid is shaped differently in these taxa. However,

this does not affect the homology of the foramen cavernosum character, and that part of the morphology is not related to the carotid as far as we can determine. Our analysis comes to different conclusions (as discussed elsewhere) from those of Broin (1991) and Lapparent de Broin (2000b), because we interpret this character is a synapomorphy of our infrafamily Erymnochelyodda, with *Peltocephalus* and *Erymnochelys* as sister taxa within that clade.

**37. PT, pterygoid flange around cavum pterygoidei:** (0) absent or very small; (1) partial; (2) complete.

*Discussion:* Figured by França and Langer (2006) and described in Gaffney et al. (2006: 603), we recognize two states, but do not order them.

**38. PT, processus trochlearis pterygoidei:** (0) absent; (1) oblique; (2) right angle.

*Discussion:* The processus trochlearis pterygoidei (figs. 23, 24, 70) is an important pleurodire synapomorphy described in Schumacher (1954, 1955a, 1955b, 1956) and Gaffney (1975b, 1979). This character is used in Gaffney and Meylan (1988), Rougier et al. (1995), Lapparent de Broin and Werner (1998), Lapparent de Broin (2000b), Fuente and Iturralde-Vinent (2001), and Gaffney et al. (2006). We have recognized two states as have a number of the above authors, and order them on the basis of state 1 occurring in the outgroup taxa and state 2 occurring only in the family Podocnemididae.

**39. SO, roof exposure:** (0) absent or slight; (1) present, small; (2) present, very large.

*Discussion:* Discussed by Meylan et al. (2009: 15), this character possibly requires three independent acquisitions with state 2 possibly being a fourth. The states could be ordered because the large extent of the supraoccipital requires the smaller state as an evolutionary predecessor.

**40. SO, horizontal plate along ventral edge of crista supraoccipitalis:** (0) absent; (1) present.

*Discussion:* This is a variable character recognized as more than a swelling along the ventral edge of the supraoccipital, but a distinct horizontal flange or plate. It is a synapomorphy for the subfamily Podocnemidinae and lost in *Erymnochelys* and *Peltocephalus.*

**41. EX, occipital condyle:** (0) basioccipital plus exoccipitals; (1) exoccipitals only.

*Discussion:* This character is described and discussed in Gaffney et al. (2006: 607). The absence of the basioccipital in the condylus occipitalis is a synapomorphy for the family Pelomedusidae but occurs elsewhere only in bothremydids and the podocnemidid, *Peiropemys.*

**42. EX, foramen jugulare posterius:** (0) closed partially; (1) closed completely.

*Discussion:* An extensive description and discussion is in Gaffney et al. (2006: 607); also see Gaffney and Wood (2002). In the present analysis, this character helps define the subfamily Podocnemidinae, which is all podocnemidids except *Bauruemys.*

**43. EX, foramina nervi hypoglossi:** (0) separated on occipital surface; (1) combined and recessed below occipital surface.

*Discussion:* In other podocnemidids the two pairs of foramina nervi hypoglossi open onto the posterior surface of the skull in clearly separated foramina. These foramina are relatively small, distinctly smaller than the foramen jugulare posterius that is just lateral to them. This condition is common throughout turtles (Gaffney, 1979) and is interpreted as the primitive condition. In the tribe Stereogenyini, however, the two foramina nervi hypoglossi are very close together and separated by a relatively thin bar of bone. Both foramina are sunk below the surface to exit as a single foramen. This single foramen is about the same size as the foramen jugulare posterius in the tribe Stereogenyini. Although the foramen jugulare posterius varies in size throughout turtles, it is distinctly smaller in the tribe Stereogenyini than in other pelomedusoides such as *Podocnemis* and *Pelusios.* The occipital aspect of the tribe Stereogenyini, then, has two equally sized, paired foramina just lateral to the condylus occipitalis (fig. 65F), but one of these is the combined foramina nervi hypoglossi and the other is the foramen jugulare posterius.

This character is absent in *Bairdemys sanchezi* and *Lemurchelys,* which require reversals. It is present in *Mogharemys* and diagnostic of the entire tribe Stereogenyini.

**44. BO, basioccipital short in ventral view, precondylar fossa very small:** (0) no; (1) yes.

*Discussion:* In *Shweboemys* the basioccipital is a small curved bone, very short anteroposteriorly, with a small amount of ventral exposure. In *Stereogenys* the basioccipital is even more displaced posteriorly and has only a slight amount of ventral exposure. This results in a very small precondylar fossa in these two taxa. The other members of the tribe Stereogenyini have larger basioccipitals, similar or identical to other podocnemidids. The character is also discussed in Meylan et al. (2009: 15)

**45. BO, basioccipital tubera width:** (0) closer to median; (1) farther from median.

*Discussion:* This feature is described and discussed in Meylan et al. (2009: 15). In the present analysis, it is a synapomorphy for the subfamily Podocnemidinae, occurring outside this clade only in the bothremydids.

**46. BO, horizontal occipital shelf:** (0) absent; (1) present.

*Discussion:* In the primitive condition, such as in *Euraxemys* and chelids (but not pelomedusids), the occipital surface is relatively flat and vertical, with a variably expressed tuberculum basioccipitale. In *Podocnemis*, *Bauruemys*, *Hamadachelys*, and the tribe Peiropemydini, there is a horizontal shelf that extends posteriorly from the base of the occiput formed almost entirely by the basioccipital and partially by the exoccipital. The character is a synapomorphy for Podocnemididae plus *Hamadachelys* and is lost in the infrafamily Erymnochelyodda.

**47. PR, ventral exposure:** (0) completely exposed; (1) partially or completely covered.

*Discussion:* See Gaffney et al. (2006).

**48. PR, pterygoid covers prootic:** (0) no; (1) partially or completely.

*Discussion:* This character is described and discussed in Gaffney et al. (2006: 610).

**49. PR, foramen posterius canalis carotici interni:** (0) in prootic; (1) in basisphenoid within cavum pterygoidei; (2) variably in pterygoid, quadrate, basisphenoid; (3) pterygoid and basisphenoid.

*Discussion:* In all the podocnemidids examined by us the foramen posterius canalis carotici interni lies inside the cavum pterygoidei, in the medial wall of the basisphenoid; possibly in some cases the prootic enters the foramen. The larger cavum pterygoidei of *Erymnochelys* and *Peltocephalus* still has a formed foramen posterius canalis carotici interni in the basisphenoid despite the erosion of much of the bone defining the foramen posterius canalis carotici interni anteriorly.

**50. OP, processus interfenestralis:** (0) exposed; (1) covered.

*Discussion:* This character is described and discussed in Gaffney et al. (2006: 611).

**51. OP, fenestra postotica:** (0) open; (1) partially or completely closed.

*Discussion:* This character is described and discussed in Gaffney et al. (2006: 612).

**52. BS, foramen nervi abducentis:** (0) small; (1) moderate to large.

*Discussion:* This character is discussed in Meylan et al. (2009: 16). A relatively large foramen nervi abducentis helps define the genus *Podocnemis*. It also occurs in *Pricemys*, but the difficulty in seeing it in most fossils precludes its wider use.

**53. BS, basisphenoid-quadrate contact:** (0) present; (1) absent.

*Discussion:* This character is described and discussed in Gaffney et al. (2006: 613).

**54. DEN, symphyseal contact:** (0) fused; (1) sutured.

*Discussion:* This character is described and discussed in Gaffney et al. (2006: 616).

**55. ART, processus retroarticularis:** (0) long and posterior; (1) short or absent; (2) long and posteroventral.

*Discussion:* This character is described and discussed in Gaffney et al. (2006: 617; see also Gaffney et al., 1998; Gaffney and Forster, 2003). The long, posteroventrally directed processus retroarticularis is a feature of the epifamily Podocnemidinura.

**56. ART, chorda tympani enclosed in processus retroarticularis:** (0) no; (1) yes.

Discussion: The absence of lower jaws for many fossil taxa precludes the more general use of this character. However, it is present in all infrafamily Erymnochelyodda for which the lower jaw is known, but also occurs in *Brasilemys* and *Euraxemys*.

**57. SP, splenial:** (0) present; (1) absent.

*Discussion:* The splenial is absent in all of the taxa included (where area is preserved) except chelids.

**58. Vertebrae, cervical centra saddle shaped:** (0) absent, procoelous; (1) completely

heterocoelic as in *Podocnemis;* (2) wide as in *Erymnochelys.*

*Discussion:* The "saddle-shaped" or heterocoelic central articulations are described and discussed in Gaffney et al. (2006: 618) with references to the earlier works. This character is a synapomorphy for the redefined, subfamily Podocnemidinae, being absent as a reversal, or third state, only in *Erymnochelys.* In our analysis, *Bauruemys* is the only taxon in the family Podocnemididae with the primitive cervical condition (see below for *Erymnochelys*). The absence of heterocoelic central articulations ("saddle-shaped") in *Bauruemys* rests on Kischlat's (1994) description and on our observations of the same material, MN V 4487, two cervicals of unknown position, but with simple, oval procoelous articular surfaces. However, other very similar cervicals are also seen among the uncataloged *Bauruemys* material in the DGM (specifically DGM uncataloged, collected 1969, Campos and Silva, carapace and plastron disarticulated with postcranial material in carapace part, including an eighth cervical vertebra).

Kischlat (1994: 348) described the two cervicals (MN V 4487) of unknown position of *Bauruemys elegans* as having simple, oval procoelous articular surfaces, that is, lacking saddle-shaped articulations. We have also examined these vertebrae and a number of similar cervicals in the uncataloged collections of the DGM, and we agree with the primitive condition of these articulations. The articulations are clearly similar to the outgroup cervicals, such as in *Euraxemys* and pelomedusids, in being a relatively simple, hemispherical, concave-convex articulation, not the more complex surface seen in *Podocnemis* and *Peltocephalus.*

Cervicals of *Lapparentemys vilavilensis* cervicals are known from a number of specimens and described by Broin (1991: 513) as "with saddle-shaped centra (like *Podocnemis* and *Peltocephalus*)." We have examined these and agree that they are the same state as in the Recent *Podocnemis* and *Peltocephalus.*

The classically termed "saddle-shape" condition is worth reexamining, particularly in view of the discovery that the Miocene *Turkanemys* has a condition similar to that in *Erymnochelys.* Cervicals four to seven of *Erymnochelys* (Vaillant, 1881; Tronc and Vuillemin, 1974) and *Turkanemys*, although not heterocoelic or saddle shaped with the curved central articulation extending posterolaterally as seen in *Podocnemis* and *Peltocephalus*, are also significantly different from the presumed primitive condition as seen in the Podocnemininae (as defined here) outgroups, such as *Bauruemys* and *Euraxemys.* The cervical articulation surfaces in *Erymnochelys* and *Turkanemys* are not simple oval articulations, but are wider than high and become V-shaped with dorsolateral extensions in the more posterior cervicals in the series. It is possible to interpret this as morphologically intermediate between the primitive condition and the "saddle-shaped" condition, but we do not make that assumption. Rather, we code this as a third state, unordered, but not the same state as the primitive condition, from which it differs considerably. The MPCs do not differ if the *Erymnochelys* and *Turkanemys* condition is coded as primitive, whether two or three states are used. Also the MPC is the same if the states are ordered.

**59. Vertebrae, second cervical biconvex:** (0) no; (1) yes.

*Discussion:* This character is described and discussed in Gaffney et al. (2006: 618).

**60. Vertebrae, cervical zygapophyses:** (0) none fused; (1) some fused.

*Discussion:* This character is described and discussed in Gaffney et al. (2006: 618).

**61. Carapace, cervical scale:** (0) present; (1) absent.

*Discussion:* This character is described and discussed in Gaffney et al. (2006: 621).

**62. Carapace, nuchal bone width:** (0) two or more times length; (1) width greater than length, but less than two times; (2) width equals length; (3) very reduced nuchal (*Araripemys*).

*Discussion:* This character is described and discussed in Gaffney et al. (2006: 621).

**63. Carapace, neural series extent:** (0) to suprapygal; (1) to costals eight; (2) to costals seven; (3) to costals six; (4) neurals discontinuous or absent.

*Discussion:* This character is described and discussed in Gaffney et al. (2006: 622). As many of the genera analyzed here lack shells,

the distribution of this character lacks specificity. However, it and the closely related character, neural number, are consistent with the *Erymnochelys* + *Peltocephalus* + tribe Stereogenyini clade, as well as a monophyletic *Podocnemis*.

**64. Carapace, neural number:** (0) eight or more; (1) seven; (2) six; (3) five or fewer.

*Discussion:* This character is described and discussed in Gaffney et al. (2006: 622). See also neural series extent character above.

**65. Carapace, keeled neurals:** (0) none; (1) some.

*Discussion:* Two species of *Podocnemis, P. sextuberculata* and *P. unifilis*, have this character, but no other characters support this grouping and it is not present in the shortest tree.

**66. Carapace, four-sided neural position:** (0) first neural; (1) second neural; (2) third neural; (3) neurals absent or discontinuous; (4) four-sided neural absent.

*Discussion:* This character is described and discussed in Gaffney et al. (2006: 623). All Podocnemididae have the first neural four sided, except *Bairdemys venezuelensis* (neurals absent) and *Bauruemys* (second neural).

**67. Carapace, costal two anterior edge thickened near buttress:** (0) no; (1) yes.

*Discussion:* Apparently present only in *Bauruemys*, Peirópolis B, and the shell taxon *Roxochelys* (see discussion in Systematics section).

**68. Carapace, axillary buttress:** (0) reaches peripheral three; (1) reaches peripheral two.

*Discussion:* This character is described and discussed in Gaffney et al. (2006: 626). In the present analysis it forms a group containing all *Podocnemis* except *P. vogli,* and occurs independently in *Cambaremys.*

**69. Plastron, axillary musk duct (1):** (0) in buttress; (1) absent in buttress.

*Discussion:* Unknown for all fossils and scored only for the living podocnemidids, it forms no groups.

**70. Plastron, axillary musk duct (2):** (0) not in bridge; (1) one opening in bridge; (2) three openings in bridge; (3) four openings in bridge.

*Discussion:* Unknown for all fossils and scored only for the living podocnemidids, it resolves some groups within *Podocnemis.* State 2 occurs in *P. sextuberculata, P. erythrocephala,* and *P. unifilis.*

**71. Plastron, mesoplastra:** (0) small and lateral; (1) absent.

*Discussion:* This character is described and discussed in Gaffney et al. (2006: 628).

**72. Plastron, pectoral scales contact mesoplastra:** (0) yes; (1) no.

*Discussion:* This character is described and discussed in Gaffney et al. (2006: 637). As currently known for this analysis, it differentiates *Lapparentemys* from all other epifamily Podocnemidinura in which the shell is known.

**73. Plastron, pectoral scales contact entoplastron:** (0) no; (1) yes.

*Discussion:* This character is described and discussed in Gaffney et al. (2006: 630). It occurs in all epifamily Podocnemidinura in which the shell is known.

**74. Plastron, pectoral scales contact epiplastra:** (0) no; (1) yes.

*Discussion:* This character is described and discussed in Gaffney et al. (2006: 636). It occurs in all members of the family Podocnemididae. It is absent in *Portezuelemys* and unknown in *Hamadachelys* and *Brasilemys.*

## CONCLUSIONS

The phylogenetic analysis (fig. 98) was made with PAUP* version 4.0b10 (Swofford, 2002) using the parsimony algorithm. All characters were run unweighted and unordered. Characters were entered and cladograms examined using MacClade version 4.05 (Maddison and Maddison, 2000). The character matrix (appendix 1) used as the basis of this analysis has 37 taxa and 74 characters. Five of these characters are parsimony uninformative. Characters 1 (presence of nasals), 57 (presence of splenial), 59 (second cervical biconvex), and 61 (cervical scale absent) are variable but absent in only one taxon, the Chelidae, the most extreme outgroup in this analysis. Character 34 (medial process of quadrate present) occurs in all taxa. These characters were included as they were used in the matrix of Gaffney et al. (2006). The PAUP* analysis of appendix 1, using both heuristic and stepwise addition (random) searches, results in 9

Fig. 98. Consensus cladogram of nine equally parsimonious cladograms of 173 steps resulting from a PAUP* analysis of 74 characters (69 informative) and 37 taxa. All characters unweighted and unordered, character matrix in appendix 1, character list in appendix 2. [F. Ippolito, del.]

equally parsimonious trees of 173 steps (fig. 98).

Although we have run all multistate characters as unordered, some arguments could be made for ordering at least some of them. These are discussed under the relevant character listed above. The possibility exists that some multistate characters should be ordered even though we have no evidence for this.

The outgroups chosen are based on the work of Gaffney et al. (2006). The Chelidae, Pelomedusidae, *Araripemys,* Euraxemydidae, and Bothremydidae are dealt with in greater detail in that paper.

The characters used here have been developed over the course of the pleurodire work by E.S.G. and P.A.M. An early version of our matrix was published in Meylan (1996) and a later version in Meylan et al. (2009). We have incorporated characters from the literature as well, particularly Lapparent de Broin (2000b), Fuente (2003), França and Langer (2006), and Romano and Azevedo (2006). Cadena et al. (2010) became available too late to be considered in our analysis, but the matrix used in that paper is similar to ours.

The family Podocnemididae consists of 20 genera and 30 species diagnosable by cranial characters (an additional shell taxon is present) of which three genera and eight species persist into the Recent fauna. The family extends from the Late Cretaceous to the Recent and occurs in North and South America, Europe, and Africa. The family Podocnemididae is reconfirmed as monophyletic, using the unique structure, a cavum pterygoidei that is formed by the basisphenoid, pterygoid, prootic, and quadrate, underlain by pterygoid and basisphenoid, among other characters.

A phylogenetic analysis analyzes 33 taxa in the Podocnemididae (37 taxa including outgroups). The resulting nine equally parsimonious cladograms are the basis for a new classification of the family. Much of our basal resolution agrees with that of França and Langer (2006), which can be modified and restated as follows: (*Bauruemys* (*Lapparentemys* (*Podocnemis* (*Peltocephalus, Erymnochelys*)))). Cadena et al. (2010) could also be restated as (*Bauruemys Lapparentemys* (*Podocnemis* (*Peltocephalus, Erymnochelys* (*Neochelys* (*Dacquemys* (*Bairdemys, Shweboemys, Stereogenys*)))))), and agreeing in its main resolution with ours as well, particulary in the resolution of the living podocnemidids as: (*Podocnemis* (*Peltocephalus, Erymnochelys*)).

### Podocnemididae

Within the family Podocnemididae, the sister taxon to all other podocnemidids is *Bauruemys elegans* (Suárez, 1969a). All other podocnemidids, the redefined subfamily Podocnemidinae Cope, 1868, are united by a long quadratojugal-parietal contact, a completely enclosed foramen jugulare posterius, wide basioccipital tubera, horizontal plate present on ventral edge of crista supraoccipitalis (except in *Peltocephalus* and *Erymnochelys*), and cervical centra saddle shaped (except in *Erymnochelys* and *Turkanemys,* which nonetheless lack the primitive condition).

### Basal Podocnemididae

A basal group of Cretaceous-Paleocene podocnemidids that are the sister group to all remaining podocnemidids are *Peiropemys mezzalirai,* n. gen. et sp., *Lapparentemys vilavilensis* (Broin), n. gen., and *Pricemys caiera,* n. gen. et sp. The remaining podocnemidids are the infrafamily Podocnemidodda Cope, 1868, new rank, that are characterized by the possession of a cheek emargination that does not reach above the level of the orbit, the medial expansion of triturating surface with a median maxillary ridge present, and the presence of accessory ridges. This group contains the living podocnemidids and a series of extinct forms, including the marine broad-jawed taxa. Meylan (1996) recognized "*Roxochelys*" (= *Lapparentemys*) as the sister group to all other Podocnemididae that were in his analysis, which excluded *Bauruemys.*

### Infrafamily Podocnemidodda

Within the Podocnemidodda, the genus *Podocnemis* is the sister group to all the remaining taxa, i.e., the magnatribe Erymnochelydand. The infrafamily Podocnemidodda is characterized by the medial expansion of the triturating surface with the median ridge,

and the presence of one or two accessory ridges on the triturating surface.

The magnatribe Podocnemidand consists only of the genus *Podocnemis.* Our resolution of the *Podocnemis* species is: (*P. vogli* (*P. lewyana* (*P. unifilis* (*P. erythrocephala* (*P. sextuberculata, P. expansa*))))). We do not consider this part of the analysis to be strongly supported as the resolution collapses into a multichotomy in one step more than the shortest resolution. Osteologically speaking, these Recent species are very similar to each other and have very conservative morphologies, even within a group that has changed little since the Late Cretaceous.

### Magnatribe Erymnochelydand

The magnatribe Erymnochelydand, with all taxa included, is diagnosed only by the reduced cheek emargination, which is reversed in *Bairdemys* and *Cordichelys. Caninemys* is the sister taxon to all remaining magnatribe Erymnochelydand, which is united by the absence of a vomer (present in *Caninemys* but also absent in most, possibly all, *Podocnemis*) and the lateral, anterolateral orbital position, both characters homoplastic in other pleurodires. However, this is primarily the effect of missing characters in these taxa and, if *Caninemys, Dacquemys,* and UCMP 42008 are excluded, collapsing these nodes, the number and consistency of characters uniting the remaining clade increases: **2,** orbits facing laterally, anterolaterally; **11,** cheek emargination slight; **30,** fossa precolumellaris very small to absent; **39,** supraoccipital roof exposure absent or slight; and **56,** chorda tympani enclosed in processus retroarticularis in lower jaw.

The condition of the cavum pterygoidei is not preserved in *Caninemys, Dacquemys,* UCMP 42008, or *Turkanemys,* so the distribution of this character is unknown for a significant number of Erymnochelydand taxa, but it is known to be present above *Turkanemys.*

Within the magnatribe Erymnochelydand the resolution of taxa can be seen in figure 98. The group above *Caninemys* and *Dacquemys* + UCMP 42008 is united by the premaxillae entering the apertura narium interna in ventral view. The group above *Caninemys, Dacquemys* + UCMP 42008, and *Turkanemys* is united by the absence of the horizontal occipital shelf.

Cervical vertebrae 4–7 of both *Erymnochelys* and *Turkanemys* are very similar to each other in being wider than high and differ from other Podocnemidinae (as defined here) in lacking the well-developed heterocoely or saddle-shaped centra. This condition could be interpreted as an intermediate between the *Podocnemis* fully heterocoelous centra that wrap around posterolaterally and the condition seen in the basal podocnemidid, *Bauruemys.* Nonetheless, our analysis still places *Turkanemys* outside *Erymnochelys* + *Peltocephalus* requiring that the wide articular condition be acquired twice, despite the proximity of these taxa in the cladogram. Again, this is only a few steps from a group containing *Erymnochelys, Peltocephalus,* and *Turkanemys.* We feel that although our MPC resolves these three taxa, in view of the missing data for *Turkanemys* it would be more realistic to conclude that the three are an unresolved trichotomy at present.

In contrast to some previous analyses, among the living taxa, our results show *Podocnemis* as the sister taxon to *Erymnochelys* + *Peltocephalus.* As constituted here, the Erymnochelydand is united only by the small to absent cheek emargination, a character subject to frequent homoplasy in turtles. However, some of the fossil taxa (for example, *Turkanemys, Caninemys, Dacquemys*) are not known for some important characters and, if only the living species are used in the analysis, *Erymnochelys* + *Peltocephalus* are united by a number of characters: **2,** orbits facing laterally, anterolaterally; **9,** jugal-quadrate contact present; **11,** cheek emargination slight; **14,** premaxillae reach apertura narium interna (also in some *Podocnemis*); **36,** anterior opening of the cavum pterygoidei large and including foramen cavernosum in roof; **39,** supraoccipital roof exposure slight or absent; **46,** horizontal occipital shelf absent; **56,** chorda tympani enclosed in processus retroarticularis; **63,** neural series extends to costals six; and **70,** axillary musk duct not in bridge.

When all taxa are included, *Peltocephalus* and *Erymnochelys* are united by the jugal-

quadrate contact and the loss of supraoccipital exposure on the skull roof. Although the jugal-quadrate contact and associated loss of cheek emargination do appear in cryptodires, it is a unique character within pleurodires. The supraoccipital character is probably subject to more individual variation than we have seen and may not be useful at this level of refinement. However, it should be noted that despite arguments for homoplasy of characters in common (Lapparent de Broin, 2000b, 2003b), there are similarities between *Peltocephalus* and *Erymnochelys* that are hard to ignore. Even the shells of the two taxa are similar. The carapace of both usually has seven neurals with costals seven and eight meeting on the midline (with some individual variation). The plastron has a pectoral-abdominal sulcus very close to and just barely contacting the mesoplastron, the pectoral scale extends onto the posterior half of the entoplastron, and the very small intergular scale just touches or barely extends onto the entoplastron. The main shell difference has to do with the gular scales, which are large and meet on the midline in *Erymnochelys* and are small and are separated in *Peltocephalus*.

The cervicals of *Erymnochelys* (Vaillant, 1881; Tronc and Vuillemin, 1974) and *Turkanemys*, although not heterocoelic or saddle shaped as in *Podocnemis*, are also not the same as the presumed primitive condition as seen in outgroups such as *Bauruemys* and *Euraxemys*. It is possible to interpret this as morphologically intermediate between the primitive condition and the "saddle-shaped" condition, but we do not make that assumption. Rather, we code this as a third state, run unordered, not the same state as the primitive condition, from which it differs considerably. The MPCs do not differ if the *Erymnochelys* and *Turkanemys* condition is coded as primitive, whether two or three states are used. Also the MPC is the same if the states are ordered.

As described above, *Peltocephalus* + *Erymnochelys* are united with remaining magnatribe Erymnochelydand by the premaxillae reaching the apertura narium interna and the absence of the horizontal occipital shelf. The group above *Peltocephalus* + *Erymnochelys* consists of an unresolved trichotomy of *Neochelys*, *Papoulemys,* and the tribe Stereogenyini. These are united by the parietal-pterygoid contact in the septum orbitotemporale.

While the relative position of *Neochelys* may rest on one character, its resolution within the magnatribe Erymnochelydand, like that of *Peltocephalus* + *Erymnochelys,* is well supported by the same characters that unite *Peltocephalus* + *Erymnochelys* with the tribe Stereogenyini. The resolution of *Caninemys* within the Erymnochelydand is not strongly supported; in only one step it becomes a multichotomy with *Podocnemis* and the infrafamily Peiropemydodda. *Neochelys-Papoulemys* and *Dacquemys*, however, are strongly supported as part of the magnatribe Erymnochelydand, as proposed earlier (Broin, 1991; Lapparent de Broin, 2000b, 2001, 2003a, 2003b).

### Tribe Stereogenyini

The tribe Stereogenyini has a dorsal process of the palatine that reaches the frontal in the septum orbitotemporale, the fossa precolumellaris is absent, and both foramina nervi hypoglossi are combined and recessed in a short canal that opens on the occipital surface. Within the tribe Stereogenyini, *Mogharemys* is the sister taxon to the well-defined subtribe Stereogenyina. Until the description of *Bairdemys* (Gaffney and Wood, 2002), the subtribe Stereogenyina consisted only of *Stereogenys* and *Shweboemys* and has been recognized as monophyletic by the common possession of a well-developed secondary palate with a midline cleft. *Stereogenys* and *Shweboemys* have been referred to as the "groupe Schweboemys [sic]" Broin (1988), the "B9 taxon" (Gaffney and Meylan, 1988), the "*Schweboemys* [sic] group" (Lapparent de Broin, 2000b), and the "*Shweboemys* Group" (Gaffney and Wood, 2002). The subtribe Stereogenyina is united by these characters: a secondary palate unique among turtles in being formed by maxillae and palatines that are separated on the midline by a narrow cleft, a palate characterized by a variably developed anterior convexity and posterior concavity, the palatine making up half or more of the secondary palate, and a fossa orbitalis with

an extensive posterior pocket behind the orbital rim enclosed by the septum orbitotemporale.

Two groups are recognized within the subtribe Stereogenyina: the infratribe Bairdemydita, which has a cheek emargination that reaches the level of the orbit (only known for one genus), a labial ridge that is high and narrow, and the angle of the front of the skull is 90° or less. The infratribe Stereogenyita has a labial ridge that is low and blunt, a pinched snout (not known for *Brontochelys*), a cheek emargination that does not reach the level of the orbit, and the angle of the front of the skull exceeds 90°.

Within the infratribe Bairdemydita the genera resolve as (*Cordichelys* (*Latentemys, Bairdemys*)) with one character, the separation of the eustachian tube by bone from the fenestra postotica, found only in *Latentemys* and *Bairdemys.* The four species of *Bairdemys* are united by a vertical flange on the ventral surface of the squamosal. Three species, *Bairdemys hartsteini, B. venezuelensis,* and *B. sanchezi* are united by the presence of a strongly convex prefrontal. Two of these, *B. hartsteini,* and *B. venezuelensis* are united by the strong anterior convexity on the palate. The resulting resolution of the group is: (*Cordichelys* (*Latentemys* (*B. winkleri* (*B. sanchezi* (*B. hartsteini, B. venezuelensis*))))).

Within the infratribe Stereogenyita, *Lemurchelys, Shweboemys,* and *Stereogenys* are united by the medial edges of the midline palatal cleft being parallel rather than curved. *Shweboemys* and *Stereogenys* are united by a number of characters and are the best supported of all the groups in the subtribe Stereogenyina. They have a very short basioccipital, a palatine-basisphenoid contact that separates the pterygoids, a dorsal process of the palatine that reaches the parietal, and a relatively long secondary palate. The resolution of the infratribe is (*Brontochelys* (*Lemurchelys* (*Shweboemys, Stereogenys*))).

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# APPENDIX 1

## Character Matrix

Asterix indicates taxa represented by shells only and deleted from analysis shown in figure 98.

Chelidae
0(01)00002000300000000010000000020201000110-
0100000000000(01)1000000(012)(024)(0123)0(023)-
0(01)??2?11

Pelomedusidae
1100001100100100000010(01)00000202010001001-
100010000000(01)1010101(12)(12)(0123)0000??1000

*Araripemys*
11000010001001000000010000000200010001000(0-
1)00000000000110101114000300??2?00

Euraxemydidae
1100100000100000000000000000010001000110000-
0001031100111101111000000??1000

Bothremydidae
1(012)00(01)000(01)00000(01)00000000(01)00(01)0-
(01)(02)0111000(12)00(01)00010102110100(01)101-
(01)1(012)(023)(123)0(014)00??10(01)0

*Portezueloemys*
?1?0??0????0????00???000???0??0?111112?????00?111-
11?1???????1?2204????1110

*Brasilemys*
?100000??0?00??000000?000?0001001111110??0000-
010011?1021?0?0121204????????

*Hamadachelys*
1100100200100?00000000000?00120211111200000-
001111110102?1?????????????1???

*Bauruemys*
1200100100100000000000010000120211212210000-
0011111101?2010?01222011???1111

*Pricemys*
?1????030?2????00000??010??0110211212211010011-
1111111?????????????????????

*Peiropemys*
1100200100200000000000010?00120211212211110-
01111111?1?????????????????????

*Lapparentemys*
1100200100200000000000010?001102112122?1010-
01?1111101020?1?0112100?0??10??

*Podocnemis erythrocephala*
1110200101101101000101010000120211222211010-
01111111110201110121100?1021111

*Podocnemis expansa*
1110220201101001000111010000110211222211010-
0111111111020111011110011111111

*Podocnemis lewyana*
1110220201101001000101010000120211212211010-
0111111111020111011?110011?31111

*Podocnemis sextuberculata*
1110220201101101000101010000110211222211010-
0111111111020111011111011121111

*Podocnemis unifilis*
1110200201100001000111010000120211212211010-
0111111111020111011111011121111

*Podocnemis vogli*
1110200101101001000100010000120211212211010-
0111111111020111011110010131111

*Turkanemys*
10002?010000010100010101??001102112?220?0100-
11?111??10211210113200????1111

*Erymnochelys*
1000200210000101000101010000120211232200010-
0101111101021121011320011001111

*Peltocephalus*
1000200410000111000101010000110211232200(01-
)100101111101021111011320010001111

*Neochelys*
10(01)0210100000101000001010000110211232201-
01001011111?1021????11(23)(12)00?0??1(01)11

*Papoulemys*
10002?0100000?0100000?01??001102112?22011100-
1011111?1?????????????????????

*Caninemys*
11002?02000000010001000100002002112?22?1010-
01111111?1?????????????????????

*Dacquemys*
10002?3100000001000111010?001102112?2221010-
0111111101?????????????????????

UCMP 42008
10002?3?100?0?010001??010?00??02112?222?0?00??-
11?11?1???????????0?????????

*Mogharemys*
?000?1??????0??100?1??0101001002112322??011010-
11111?1?????????????????????

*Brontochelys*
1000?1?????????2001001220?10????112322???110101-
111?01?????????????????????

*Lemurchelys*
1000????????01120010011201102?021123220??1001-
011111?1?????????????????????

*Shweboemys*
1000?1?????001121010011211?1????112?22???1111?-
11?????????????????????????

*Stereogenys*
10002103??0?0?12101001121111200211232201011-
1101111101021?????????????????

*Latentemys*
?000?1?????00??20000012201101?121123220?01101-
01111101?????????????????????

*Cordichelys*
?00021030010010200000122011?100211232201011-
01011111?1??????113200????1111

*Bairdemys hartsteini*
1001210300?10102010001220?1020121123220?011-
01011111?1????1???????????????

*Bairdemys venezuelensis*
1001210300110102010001220110201211232201011-
01011111?102??????143031???1111

*Bairdemys sanchezi*
1001210?0011010200000?220?102012112??2010100-
1011111?1?????????????????????

*Bairdemys winklerae*
10002?0?0?1101220?000?22???0?012112??2?????010-
11?1?????????????????????????

**Cambaremys*
?????????????????????????????????????????????????????????-
?????13210010??11??

**Stupendemys*
?????????????????????????????????????????????????????????-
??1??1???0?????11??

**Kenyemys*
????????????????????????????????????????????????????????????????-
?????122210?0??1111

## APPENDIX 2

### Character List

See Character Description section for more precise characterization of states.

1. NA, nasals: 0, present; 1, absent.
2. FR, orbital position: 0, facing laterally, anterolaterally; 1, facing dorsolaterally; 2, facing dorsally.
3. FR, interorbital groove: 0, absent; 1, present.
4. FR, prefrontal/frontal: 0, flat or slight convex; 1, strongly convex dorsally.
5. PAR, quadratojugal-parietal contact: 0, absent; 1, short contact; 2, long contact.
6. PAR, parietal-pterygoid contact in septum orbitotemporale: 0, absent; 1, present and wider; 2, present and narrower.
7. PAR, temporal emargination: 0, moderate to absent; 1, extreme, as in *Pelusios;* 2, shallow, cheek emargination extensive; 3, emargination absent due to expanded parietal/supraoccipital.
8. PAR, interparietal scale: 0, absent; 1, equilateral triangle; 2, elongate triangle; 3, parallel sided; 4, broad posteriorly.
9. JU, jugal-quadrate contact: 0, absent; 1, present;
10. JU, jugal-parietal contact: 0, absent; 1, present.
11. JU, cheek emargination: 0, slight; 1, reaches level of orbit; 2, reaches above level of orbit; 3, reaches above quadrate.
12. SQ, ventral vertical flange: 0, absent; 1, present.
13. PO, size: 0, equal to orbit; 1, smaller than orbit.
14. PM, premaxillae reach apertura narium interna: 0, no; 1, yes.
15. PM, pinched snout: 0, absent; 1, concave outline near premaxilla-maxilla contact, snout not elongated; 2, concave outline posterior to premaxilla-maxilla contact, snout elongated.
16. MX, medial expansion of triturating surface: 0, absent; 1, present, forming median maxillary ridge; 2, secondary palate with midline cleft.
17. MX, secondary palate long: 0, no; 1, yes.
18. MX, triturating surface convexity: 0, absent or shallow; 1, deep.
19. MX, labial ridge: 0, high and narrow; 1, low and thick.
20. MX, accessory ridges: 0, absent; 1, one or two.
21. MX, meet broadly on midline: 0, no; 1, yes.
22. VO, vomer: 0, present; 1, absent.
23. PAL, medial edges of palatal cleft: 0, absent; 1, parallel; 2, curved.
24. PAL, palatine extent in triturating surface: 0, narrow or absent; 1, moderate, but much less than maxilla extent; 2, large, equal or slightly less than maxilla extent.
25. PAL, dorsal process of palatine contacts parietal in septum orbitotemporale: 0, no; 1, yes.
26. PAL, dorsal process reaches frontal: 0, no; 1, yes.
27. PAL, fossa orbitalis posterior pocket: 0, absent; 1, present in septum orbitotemporale.
28. PAL, palatine-basisphenoid contact separates pterygoids: 0, no; 1, yes.
29. QU, antrum postoticum: 0, large; 1, smaller; 2, smallest and slitlike.
30. QU, fossa precolumellaris: 0, very small to absent; 1, present but shallow; 2, deep and well defined.
31. QU, eustachian tube separated from fenestra postotica:0, no; 1, yes.
32. QU, incisura columellae auris: 0, no posterior bony restrictions; 1, eustachian tube separated from stapes by bone or narrow fissure; 2, eustachian tube and stapes enclosed or nearly enclosed by bone.
33. QU, quadrate-basioccipital contact: 0, absent; 1, present.
34. QU, medial process reaches braincase: 0, absent; 1, present.
35. PT, cavum pterygoidei: 0, absent; 1, partial; 2, complete.
36. PT, anterior opening of cavum pterygoidei: 0, absent; 1, small opening; 2, moderate opening; 3, large opening with foramen cavernosum in roof.
37. PT, pterygoid flange around cavum pterygoidei: 0, absent or very small; 1, partial; 2, complete.
38. PT, processus trochlearis pterygoidei: 0, absent; 1, oblique; 2, right angle.
39. SO, roof exposure: 0, absent or slight; 1, present, small; 2, present, very large.
40. SO, horizontal plate along ventral edge of crista supraoccipitalis: 0, absent; 1, present;
41. EX, occipital condyle: 0, basioccipitals plus exoccipitals; 1, exoccipitals only.
42. EX, foramen jugulare posterius: 0, closed partially; 1, closed completely.
43. EX, foramen nervi hypoglossi: 0, separated; 1, combined and recessed.
44. BO, basioccipital very short: 0, no; 1, yes.
45. BO, basiocipital tubera width: 0, closer to median; 1, farther from median.
46. BO, horizontal occipital shelf: 0, absent; 1, present.
47. PR, ventral exposure: 0, completely exposed; 1, at least partially covered.
48. PR, pterygoid covers prootic: 0, no; 1, at least in part.
49. PR, foramen posterius canalis carotici interni: 0, in prootic; 1, in basisphenoid within cavum pterygoidei; 2, variably in pterygoid, quadrate, basisphenoid 3, pterygoid and basisphenoid.
50. OP, processus interfenestralis: 0, exposed; 1, covered.
51. OP, fenestra postotica: 0, open; 1, at least partially closed.
52. BS, foramen nervi abducentis: 0, small; 1, moderate to large.
53. BS, basisphenoid-quadrate contact: 0, present; 1, absent.
54. DEN, symphyseal contact: 0, fused; 1, sutured.

55. ART, processus retroarticularis: 0, long and posterior; 1, short or absent; 2, long and posteroventral.
56. ART, chorda tympani enclosed in processus retroarticularis: 0, no; 1, yes.
57. SP, splenial: 0, present; 1, absent.
58. Vertebrae, cervical centra saddle shaped: 0, absent, procoelous; 1, completely heterocoelic as in *Podocnemis;* 2, wide as in *Erymnochelys.*
59. Vertebrae, second cervical biconvex: 0, no; 1, yes.
60. Vertebrae, cervical zygapophyses: 0, none fused; 1, some fused.
61. Carapace, cervical scale: 0, present; 1, absent.
62. Carapace, nuchal bone width: 0, width 2 or more times length; 1, width greater than length but less than 2 times; 2, width equals length; 3, width less than length; 4, nuchal retracted, not contacting peripheral bones (*Araripemys* condition).
63. Carapace, neural series extent: 0, to suprapygal; 1, to costals 8; 2, to costals 7; 3, to costals 6; 4, neurals discontinuous or absent.
64. Carapace, neural number: 0, 8 or more; 1, 7; 2, 6; 3, 5 or fewer.
65. Carapace, keeled neurals: 0, none; 1, some.
66. Carapace, four-sided neural: 0, first neural; 1, second neural; 2, third neural; 3, neurals absent or discontinuous; 4, four-sided neural absent, neurals.
67. Carapace, costal two anterior edge thickened near buttress: 0, no; 1, yes.
68. Carapace, axillary buttress: 0, reaches peripheral 3; 1, reaches peripheral 2.
69. Plastron, axillary musk duct (1): 0, in buttress; 1, absent in buttress.
70. Plastron, axillary musk duct (2): 0, not in bridge; 1, one opening in bridge; 2, three in bridge; 3, four in bridge.
71. Plastron, mesoplastra: 0, small and lateral; 1, absent.
72. Plastron, pectoral scales contact mesoplastra: 0, yes; 1, no.
73. Plastron, pectoral scales contact entoplastron: 0, no; 1, yes.
74. Plastron, pectoral scales contact epiplastra: 0, no; 1, yes.

## APPENDIX 3

### MEASUREMENTS OF PODOCNEMIDID SKULLS

**(See Gaffney et al., 2006: 685, fig. 315 for positions of measurements. D1 is left orbital width; D2 is right orbital width; J1 is height of left orbit.)**
**All measurement in mm.**

| | A | B | C | D(L) | D(R) | E | F | G | H | I | J(L) | J(R) | K | L | M | N | O |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Brontochelys gaffneyi* BMNH R.8570 | 106.1[a] | 85.4[a] | 20.3[a] | ? | 27 | 22.6 | 6.3 | 59.5[a] | 54.8 | 101.3[a] | 25.6 | 26.5 | 52.3[a] | 25.9 | 36 | 53.1 | ? |
| *Mogharemys blanckenhorni* BMNH R.8440 | ? | 76.0[a] | ? | ? | ? | ? | 13.1 | 43[b] | 40[b] | 70 b | 15.5 | 15.8 | 31[a] | ? | 19.2 | 33.1 | 58[b] |
| *Cordichelys antiqua* YPM 7457 | 65.5 | 62.4 | 15.9 | 16.7 | 16.3 | 10.8 | 2.8 | 38.9 | 32.2 | 78.8 | 12.6 | ? | 30.4 | 12 | 21.5 | 28.2 | 63.6 |
| *Lemurchelys diasphax* DPC 6425 | 103 | 98.0[b] | 25.4 | 22.7 | 22.9 | 16.3 | 6.2 | 63.8 | 56 | 108.6[a] | 16.3 | 15.1 | 49.8 | 15.3 | 36.1 | 40.8 | 97.9 |
| *Latentemys plowdeni* BMNH R.11998 | 83.2[a] | 75.1[b] | 21.7 | 20.7 | ? | 17.1 | 6.3 | 48.8 | 40.7 | 70.2[a] | 15.1 | 14.6 | 36 | 13.7 | 23.2 | 31.7 | 75.0[a] |
| *Stereogenys cromeri* AMNH 14735 (cast of CGM holotype) | 75.5[a] | 97.5 | 20.2 | 19.1 | 19.1 | 17.4 | 16.8[a] | 51.1[a] | 45.9[a] | 90.3 | 11.8[a] | 8.0[a] | 33.6[a] | 12.5 | 30.4 | 40.5 | 77 |
| *Shweboemys pilgrimi* BMNH R.8432 | 96.5[a] | 78.8[a] | 24.2 | 20.6 | 20.2 | 17.4 | 20 | ? | 61 | 86.4[a] | 20.7 | 17.7 | 44.6[a] | 18.5 | 36.8 | 42.1 | ? |
| *Peiropemys mezzalirai* MCT 1497-R | 85.5[a] | 78.1 | 15 | 19.4 | 18.8 | 16.0[b] | 11.0[b] | 42.7 | 40.0[b] | 95.6 | 18.7 | ? | 38.6 | 9.4 | 16.7 | 38.9 | 69.5 |
| *Pricemys caiera* MCT 1498-R | ? | 100.6[b] | ? | ? | ? | ? | ? | 49.6 | ? | ? | ? | ? | 42 | 12.2[b] | 18.8 | ? | ? |

[a] Damaged.
[b] Estimate.